BIOLOGY, MOVEMENT BEHAVIOUR AND SPATIAL DYNAMICS OF AN EXPLOITED POPULATION OF SMOOTHHOUND SHARK *MUSTELUS MUSTELUS* AROUND A COASTAL MARINE PROTECTED AREA IN SOUTH AFRICA

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DECLARATION

I hereby declare that all the work presented in this thesis is my own, except where otherwise stated in text. This thesis has not been submitted for a degree at any other university. Chapter 3 was published in 2013, the details of which are provided below. I hereby acknowledge co-author contribution with editing of the manuscript published in *African Journal of Marine Science.*

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Signed by candidate

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For Don and Josie

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CONTENTS

ABSTRACT

Aspects of the life-history, movement in relation to a Marine Protected Area (MPA) boundary, and short and long-term spatial behaviour in relation to environmental preferences of *Mustelus mustelus* were studied in the Saldanha Bay region on the west coast of South Africa. The overarching aim of this thesis was to examine the biological and ecological circumstances under which a MPA could provide effective protection to a commercially caught coastal shark from fishing activity. The pigmentation, reproductive biology, diet, growth and maturity of *Mustelus mustelus* was examined from 217 ranging from 381 to 1734 mm TL and 467 to 1267 mm TL for females and males, respectively. Sharks in the bay represented the largest females and males recorded worldwide. The seasonal changes in oocytes and testes development, embryo length and the occurrence of near-term and post-partum females indicated that female parturition and ovulation occurs between November and December after a gestation period of 10-11 months. The presence of juveniles, neonates and pregnant females inside the Langebaan Marine Protected Area indicates it to be a nursery ground for this species. The largest part of the diet of *M. mustelus* consisted of three species of crustaceans: *Hymenosoma orbiculare*, *Upogebia africana*, *Callichirus kraussi*. No ontogenetic shift in diet was found for *M. mustelus* from Langebaan Lagoon. *M. mustelus* grow relatively rapidly, matured early (between 3 and 6 years) and attained a maximum observed age of 13 years.

The movements of individual *Mustelus mustelus* in and adjacent to a small closed area (Langebaan Lagoon MPA, 34 km^2) situated on the West Coast of South Africa were investigated over two years using acoustic telemetry. Sharks spent the majority of the time (in hours, average 79%) inside the Langebaan Lagoon MPA, and some sharks (n = 2 of 15 recorded during a full year) did not leave the reserve during the observation period. Time

spent inside the closed area and the number of crossings of its boundary was strongly influenced by season. Sharks concentrated inside the closed area during summer, while they were widely distributed throughout the study area during winter months. A combination of shallow and sheltered waters in close proximity to the Saldanha Bay port and other boat-access points would normally make this summer aggregation highly vulnerable to fishing activity. The residency of *M. mustelus* within the closed area suggests that spatial protection may be effective for this species.

Acoustic telemetry and *in situ* environmental data were used to investigate movement of *M. mustelus* in relation to changing environmental conditions over long (seasonal) and short (20 min) time scales. Results of Generalised Additive Mixed Modeling (GAMMs) indicated no significant influence of tide or moon phase and only a weak influence of diel period on movement and direction of movement. The thermal preference for *M. mustelus* was between 18 and 22 °C as determined by GAMMS. Absolute temperature and the relative change in temperature at the shark's position were the best predictors for shark movement and its direction in summer, explained 4.4 and 42.7 % of the deviance, respectively. This study provided evidence that *M. mustelus* inside the embayment decide their position within their area of residency according to their thermal preference and that temperature change constitutes the trigger that determines movement direction.

This study confirms that *M. mustelus* are resident within the Saldanha embayment and distinct by diet, life-history parameters and colouration from stocks elsewhere. *M. mustelus* from this group are more fecund and larger in body size than those from all other populations globally, possibly due to the favourable temperature conditions in the warm sheltered lagoon and the existence of a MPA closed to fishing which includes preferred habitat for all life-

history stages of this species. In the absence of a comprehensive stock assessment and species-specific management, well-positioned closed areas that include preferred habitat can aid the sustainability of coastal shark fisheries.

GLOSSARY

Term	Description
Area Closures	The closure to fishing by particular gear(s) of an entire area/ fishing ground, or part of it, for the protection of a section of the population (e.g. spawners, juveniles), the whole population, or several populations. The closure is usually seasonal but could be permanent.
Bag limit	The number of a species that a person can legally take in a day or trip.
Bather protection programme	A sequence of shark gill nets and drumlines (floats with sequence of hooks) deployed off selected beaches along the KZN coastline to catch sharks for the purpose of bather protection
Beach-seine net fishery	Nets set from land and used to surround and area of water. Net is operated by two ropes fixed to ends, used for hauling it in and for herding fish into the nets.
Catch per Unit Area (CPUE)	The quantity of fish caught (weight used in SA) with one standard unit of fishing effort; e.g. weight of fish per 1000 hooks, or weight of fish taken by person. CPUE is often considered an index of fish abundance.
Closed Area	Geographic area with discrete boundaries that has been designated to enhance the conservation of marine resources. This includes MPA-wide restrictions on use of zones such as fishery and ecological reserves to provide higher levels of protection. Can have different zones with different degrees of protection
Closed Season	. Protection of area on a seasonal basis, allowing for the protection of fish during vulnerable periods, e.g. aggregations or spawning events.
Commercial prohibition	Any species of fish/ shark that a specific fishery is not specifically allocated or authorized to retain for commercial purposes, generally not applied to subsistence or recreational purposes.
Demersal trawl fishery	Trawl nets towed by vessel along the sea floor, nets are shaped like a cone or funnel with a wide opening separate by otter boards to catch fish. This fishery targets deep and shallow water hake.
Gillnet fishery	Fish is gilled, entangled or enmeshed in the net, depending on the minimum stretched-mesh size. Gear can be used on the surface if set with floats or fixed to the bottom with anchors.
Hake longline fishery	Set longlines consisting of a main line, to which snoods are attached with baited hooks set at regular intervals. Gear is weighted to ensure that hooks lay along or above the ocean floor. This fishery targets deep water hake.
ICCAT	International Commission for the Conservation of Atlantic Tuna

IOTC	Indian Ocean Tuna Commission
Line fishery	Simple hook-and-line fishing system (excluding the use of longlines and drumlines) with a limit of 10 hooks. Fishery is entirely boat based.
Marine Protected Area (MPA	Geographic area with discrete boundaries that has been designated to enhance the conservation of marine resources. This includes MPA-wide restrictions on use of zones such as fishery and ecological reserves to provide higher levels of protection. Can have different zones with different degrees of protection.
Midwater trawl fishery	Trawling nets towed by a vessel through the water column to catch small pelagic fish.
Octopus fishery	Plastic unbaited octopus pots with one entrance set on the bottom, connected by buoy lines to buoys on the surface. Targets octopus by providing a midden.
Patagonian toothfish fishery	Set longlines consisting of a main line, to which snoods are attached with baited hooks set at regular intervals. Gear is weighted to ensure that hooks lay along or above the ocean floor. This fishery targets Patagonian toothfish.
Pelagic longline	Drifting longlines kept near the surface at a certain depth by means of regularly spaced floats. Longlines set with a Lindgren Pitman spool with an average of 1000 baited hooks. Targets tuna and tuna like fish.
Prawn trawl fishery	Similar gear to trawl. Targets prawns.
Recreational line fishery	Simple hook-and-line fishing system (excluding the use of longlines and drumlines) with a limit of 10 hooks. Catch is for recreational or subsistence purpose only.
Rocklobster fishery	Baited square wire/ plastic traps with one entrance set on the bottom, connected by buoy lines to buoys on the surface to show their position. Targets rocklobster.
Shark directed longline fishery	Drifting longlines kept near the surface at a certain depth by means of regularly spaced floats. Longlines set with a Lindgren Pitman spool with an average of 1000 baited hooks. Targets pelagic sharks.
Small pelagic fishery	Purse-seine net which is a net set from a vessel surrounding an area of water with a long net with a bag at the center. The net is operated by two ropes fixed to its ends, used for creating the "purse" when hauling it in and herding fish into it. Targets small pelagic fish.
Total Allowable Catch (TAC)	The annual recommended or specified regulated catch for a species or species group. The fisheries management agency (regional, national or RFMO) sets the TAC from acceptable biological catch.
Total Allowable Effort (TAE)	Management of marine fisheries through rights-based management for fishing effort, and more broadly, management by regulating effort rather than catch. I.e. maximum number of vessels allowed

Tuna pole fishery	Rigid pole of 2 to 3 m and a short baited line and a strong short line at the extremity of which hangs a barbless baited / feathered jig. Pole is held by fishermen. Targets tuna.
Upper Precautionary Catch Limit (PUCL)	The maximum allowable amount of a species or species group, by weight that a fishery may take and retain, possess or land during a period of time.
Whelk fishery	Ring nets baited in the center, connected by buoy lines to buoys on surface.

*Description of gear updated from Nédélec and Prado, 1990. Fisheries management terms updated from Blackhart *et al.*, 2006.

CHAPTER 1: GENERAL INTRODUCTION

Fish abundance declined dramatically in the twentieth century. Just over half of the 445 fish stocks assessed by the FAO, which represent 80% of global catches, were either *collapsed* or *overexploited* in 2010 (Froese *et al.*, 2012). To compensate for the loss of teleost production, in many instances fishing effort shifted towards the less valuable chondrichthyans, which are now either a directed catch or by-catch in almost every marine fishery (Shotton, 1999; Stevens *et al*., 2000). Chondrichthyans are harvested for their meat, fins, skin, gill rakers, cartilage and livers (Clarke 2002, Hareide *et al*., 2007, Davidson *et al.*, 2015, Jabado *et al.*, 2015).

In the 1950s the global reported chondrichthyan catch was 270 000 t p.a., but by 2011 the harvest had increased to 700 000 t p.a. (FAO, 2011). Most shark-directed fisheries are characterised by a history of overharvest and stock decline, with only a few showing limited recovery (Bonfil, 1994; Stevens *et al.*, 2000; Dulvy *et al*., 2017; Simpfendorfer and Dulvy, 2017). The most notable examples of "boom and bust" among chondrichthyan fisheries are the Californian *Galeorhinus galeus* fishery (Ripley, 1946), the Norwegian *Lamna nasus* fishery (Bonfil, 1994; Hurley, 1998; Campana *et al*., 2008) the North Atlantic *Squalus acanthias* fisheries (Ketchen, 1986; Rago *et al*., 1998), the common skate fisheries for *Dipturus batis* in the Irish Sea (Brander, 1981) and *Dipturus laevis* in the North-West Atlantic (Casey and Myers, 1998). Of the 1 041 chondrichthyans assessed by the International Union for Conservation of Nature (IUCN) Red List in 2014, 17.4% are classified as Threatened, 2.4% as Critically Endangered, 4.1% as Endangered, 10.9% as Vulnerable, 12.7% as Near Threatened and 23.2% as Least Concern, with almost half of the assessed species being classified as Data

Deficient meaning that there is insufficient data to assess their status (Dulvy *et al*., 2014). However, not all chondrichthyan fisheries are unsustainable. Approximately 9% of the current global catch of sharks of varying life-history strategies are sustainably harvested regardless of sufficient fisheries management (Simpfendorfer and Dulvy, 2017). However, strong timely science-based management generally results in sustainable fisheries for sharks (Walker, 1998, Stevens *et al.*, 2000b, Punt *et al.*, 2005, Musick and Musick 2011; Simpfendorfer and Dulvy 2017).

Stock assessments have been identified as a vital precursor to effective regulation of fish and shark stocks (Worm *et al.,* 2009). In general, however, only highly valued, target species that have been fished extensively and over a long period have been assessed (Froese *et al*., 2012). Apart from national assessments, Regional Fisheries Management Organizations (RFMOs) such as Indian Ocean Tuna Commission (IOTC), International Commission for the Conservation of Atlantic Tunas (ICCAT), Inter-American Tropical Tuna Commission (IATTC), and Western and Central Pacific Fisheries Commission (WCPFC) conduct assessments on chondrichthyans either by way of fitting models, or by analysis of standardization of CPUE time series, but again these are limited to a select suite of commercially valuable or threatened species. In contrast, low value chondrichthyans stocks, and those that have not withstood decades of fishing, have not been assessed (Lack and Sant, 2009; Froese *et al*., 2012). Species with low economic value seldom attract large funding resources for research and monitoring. At issue here are the large costs associated with regular surveys, in relation to the value of the fishery.

Assessments of chondrichthyans are often complicated by their status as by-catch in multi-species fisheries (Stevens *et al.*, 2000). Shark by-catch is not always properly

recorded and fishery regulations are typically based on more productive teleosts (Stevens *et al.*, 2000, Ferretti *et al.*, 2008, 2010). Sharks are regarded by many as inherently less fecund and therefore less capable of withstanding fishing pressure (Holden, 1973, Casey and Myers 1998, Stevens *et al.*, 2000; Simpfendorfer and Dulvy, 2017; Bradshaw *et al.*, 2018). Poor data leads to increased uncertainty in shark stock assessments and difficulty to objectively determine the degree of fishing pressure stocks are able to withstand. Paucity of historical data also means that a stock collapse is difficult to predict or confirm. In the absence of fishery data or where quality of fishery data may be of issue, demographic models based on life-history parameters and mark recapture models are used to estimate vulnerability to exploitation (Cortés, 1998, 2008; Bradshaw, 2005; Meekan *et al*., 2006).

MANAGEMENT OF CHONDRICHTHYAN FISHERIES GLOBALLY

Despite historical mismanagement and collapse in many regions, sustainable fisheries have been documented, especially in cases where targeted species are resilient to fishing pressure or where timely management interventions were introduced (Bonfil, 1994; Pauly *et al*., 1998; Stevens *et al.*, 2000; Prince, 2005; Dulvy *et al.*, 2017; Simpfendorfer and Dulvy 2017). An example pertinent to this thesis would be *Mustelus antarcticus* fished by the Australian Southern Shark Fishery and its resilience to industrial fishing. Prince (2005) showed that due to the "gauntlet nature" of this fishery targeting several year-classes of pups, juveniles and sub-adults, the large adults escape fishing pressure. The resilience of this fishery is attributed to the release of large mature sharks that are more fecund than smaller mature sharks of the same species. Similarly, the sustainability of *C. obscurus* caught in the same fishery has been attributed to the targeting of small sharks (McAuley *et al*., 2007). Management interventions aimed at restricting fishing mortality to a few juvenile age-classes resulted in the observed resilience. This strategy may only be effective for fast growing sharks with high natural mortality at smaller sizes. Practically this can be achieved if the fishery only selects certain size classes such as those caught in mesh size-controlled gillnet fisheries or if there is a market demand for a specific size class. This is the case in South Africa, where meat from coastal sharks generally over 1.3 m are commercially less valuable (da Silva *et al.*, 2015).

MANAGEMENT OF CHONDRICHTHYAN FISHERIES IN SOUTH AFRICA

In South Africa, chondrichthyans are harvested as target or by-catch species in 9 of its 17 commercial fisheries (da Silva *et al.*, 2015). Commercial-scale exploitation of chondrichthyans began in the 1930s (von Bonde, 1934). After World War II, an increase

in demand for natural vitamin A obtainable from shark livers resulted in a decline of *Galeorhinus galeus* first detected in the late 1940s (Davies, 1964; Kroese and Sauer, 1998). Demand decreased when a synthetic vitamin A substitute became widely available in 1947 (Milas, 1947). Interest in sharks and shark-directed fisheries re-ignited in 1992 when a shark-directed longline fishery aimed at catching both demersal and pelagic sharks was promoted (Kroese and Sauer 1998). In 2012, the most recent year for which chondrichthyan catches have been compiled, total landings were estimated at 2527 t dressed weight for all ~100 species of chondrichthyans (da Silva *et al.*, 2015). Directed fisheries for shark include the demersal shark longline fishery, pelagic longline fishery, linefishery, beach-seine net ('treknet') fishery, gillnet fishery, recreational linefishery and the bather protection programme. Non-directed fisheries include the demersal trawl fisheries (inshore and offshore), hake longline fishery, prawn trawl fishery, and small-pelagic and mid-water trawl fisheries. Infrequent shark by-catch is reported from the tuna-pole, patagonian toothfish, octopus, whelk and rock-lobster-trap fisheries, but these are seldom retained.

Despite large annual landings, estimated at 3375 t, 3241t and 2527 t for 2010, 2011 and 2012, respectively (da Silva *et al.*, 2015), only a few studies local studies addressed the fishery dynamics of chondrichthyan species. One of these provided a full stock assessment (da Silva, 2007) whereas another two stopped at providing standardised CPUE time-series (Jolly 2011; Groeneveld *et al*., 2014). The da Silva (2007) assessment showed that *Mustelus mustelus* was optimally- or marginally over-exploited. Comprehensive stock assessments on South African chondrichthyans are hindered by data limitations, particularly short historic fishery-dependent catch return data and fishery-independent data survey data, limited species-specific reporting in certain

fisheries and sporadic collection of size frequency data. Due to economic incentives to manage main targets of fisheries and better fishery data collected on target species, target fisheries are generally easier to assess and manage than by-catch fisheries (Oliver *et al*., 2015).

Demographic modelling of *Triakis megalopterus* suggests high vulnerability to fishing (Booth *et al.*, 2010). McCord (2005) applied the per-recruit model to *G. galeus*, indicating that the South African stock was optimally exploited. Mark-recapture models applied to *Carcharias taurus* using tag and recapture data showed stable catch trends (Dicken *et al.*, 2007). Mark-recapture models of the *Carcharodon carcharias* using photo-identification techniques showed that there has not been a substantial increase in numbers since National protection in 1990s (RSA, 1992; Towner *et al.*, 2013).

CHONDRICHTHYAN FISHERY REGULATIONS IN SOUTH AFRICA

Chondrichthyan fisheries in South Africa are managed by way of input controls in the demersal shark longline fishery (Total Allowable Effort or TAE), linefishery (TAE and, area closures), beach-seine net ('treknet') fishery (TAE, and area closures), gillnet fishery (TAE and area closures) and the bather protection programme (TAE, closed season). Output controls apply in the pelagic longline fishery (Precautionary Upper Catch Limit or PUCL), linefishery (bag limits), and the recreational fishery (commercial prohibition).

From the above it is evident that a Total Allowable Catch (or TAC) is not applied to any chondrichthyan fishery, most likely for the following two reasons. Firstly, stock assessments are uncertain or not available at all, and secondly, large volumes are caught

as by-catch across multiple fisheries and cannot be practically controlled by way of TACs. The PUCLs are a relatively new development in the inshore trawl and pelagic longline fishery, aimed at controlling by-catch volumes, but the concept has yet to be shown to be an effective measure (DAFF, 2010; Greenstone, 2013). TAEs are the default management option for all except the recreational fishery. Although the details may differ from one fishery to another, TAEs generally have been set to some historical level deemed to be sustainable. These are adjusted on the basis of evidence to the contrary. Effort generally refers to the number of fishing boats active in any given year. TAEs have effectively prevented effort creep, notwithstanding technological development.

Species-specific output controls are in place for a handful of species. Bag limits of chondrichthyans are only in place for the recreational fishery with a total of one individual of each shark species per angler per day, with the exception of prohibited species. Since 2005 a number of iconic and popular chondrichthyan species including *C. carcharias*, *Poroderma pantherinum*, *C. taurus*, *T. megalopterus*, *Cetorhinus maximus*, *Rhyncodon typus* and sawfishes Pristidae have been prohibited from capture and sale in all fisheries (RSA, 2005). The *de facto* conservation status of these prohibited species may vary substantially. Whereas *C. carcharias* are abundant, *Pristis* spp. have been extinct in SA since 1999 (Everett *et al*., 2015). Due to low capture rates in all fisheries (<10 t p.a.), CITES Appendix II listing, and limited significance to the socio-economic wellbeing of fishers, certain species are prohibited from capture by way of permit conditions applicable certain fisheries. These include *Sphyrna* spp., *Carcharhinus falciformis*, *Manta* spp., *C. longimanus*, *Alopias* spp., and *C. taurus*.

There are 22 Marine Protected areas (MPAs) with varying degrees of fishery management restrictions, including no take areas, and areas where certain types of extraction and uses are permitted (Lombard *et al*., 2005; Fernández, 2011). The total surface area within the exclusive economic zone (EEZ) is 1 071 883 km^2- 0.16 % falls into 'no take' MPAs, 0.23 % falls under other types of MPAs and 98.65 % is not under protection by an MPA (Lombard *et al*., 2005). Lombard *et al*., (2004) concluded that marine biodiversity was not fully protected by this array of MPAs. However, despite the small area covered, benefits of MPAs have been shown for a variety of species throughout South Africa (Bennett and Attwood, 1991; Attwood and Cowley, 2005; Kerwath *et al.*, 2008, 2009, 2013; Hedger *et al*., 2010). For the remainder of the thesis no take MPAs are referred to as closed areas.

THE SCIENCE BEHIND FISHERY CLOSED AREAS

Closed areas are advocated as a method to sustain fisheries (Denny and Babcock 2004, Worm *et al.*, 2009), either by way of protection of spawner-biomass or protection of vulnerable life-history stages and reseeding of adjacent areas (Gell and Roberts, 2003; Pelc *et al.*, 2009). Many socio-economic and biological factors influence the degree of protection that closed areas provide to different species. The success of a proposed closed area is difficult to predict even when ignoring factors relating to enforceability and fisheries compliance and focusing purely on the biological and ecological criteria. Therefore, the hypotheses to investigate involve which biological and ecological criteria should be applied when predicting the success of a closed area (Götz *et al*., 2013). The degree of protection provided by a closed area depends largely on the movement behaviour and life-history of the species of interest (Botsford *et al.*, 2003). Closed areas

can only be effective if the individuals of the species they intend to protect are resident within the closed area or, if migratory, the closed area is strategically placed to protect crucial life-history stages such as spawning/ pupping and nursery areas (Gell and Roberts, 2003; Kerwath *et al.*, 2009). Alternatively, depending on their life-history, a closed area may only be effective if it protects larger, more fecund adults. Global closed areas in general have been implemented opportunistically in the absence of rigorous management or conservation plans (Hearn *et al.*, 2010; Bond *et al.*, 2012).

Few studies have evaluated closed areas as an effective conservation tools for sharks (Garla *et al.*, 2006a; Bond *et al.*, 2012; Knip *et al.*, 2012). Existing studies focus on charismatic Carcharhinid sharks in tropical regions that complete their life-cycle within coral reef ecosystems (Garla *et al*., 2006a; Garla *et al.*, 2006b; Robbins *et al.*, 2006; Heupel *et al.*, 2009; Bond *et al*., 2012). These studies can generally be divided into two groups; those that use acoustic telemetry or those that use catch data. Studies using acoustic telemetry generally use an acoustic array arranged across an atoll or reef to cover the entire study area. The design of the array generally limits the analysis of the habitat use to presence or absence inside or outside the closed area (Heupel and Simpfendorfer, 2005a; Bond *et al*., 2012) or use kernel density analysis to estimate habitat use from the receivers where a particular shark was recorded (Speed *et al*., 2016). This design also limits the ability to quantify the protection provided by the closed area with any degree of accuracy. Improved results can be achieved through thoughtful selection of study site such as a small linear bay with the closed area boundary representing a narrow area easy closed off with a number of receivers in order to quantify the degree of protection. Furthermore, the addition of a double line of receivers allows for the examination of movement directionality which provides further

information regarding the effectiveness of a closed area. Such studies are rare in teleosts and non-existent in sharks. Instead of investigating the effectiveness of a closed area in protection of a particular species, it might be better to investigate which biological and ecological criteria are important to the species one is intending to protect and to determine which combination of factors would increase protection. Studies using catch data usually compare abundance or CPUE of sharks inside and outside the closed area to estimate its protection, therefore they are unable to investigate movement out of the area. Limitations of these methods result in the inability to quantify closed area performance over time. Additionally, as funding is limited given the high costs of telemetry, public concern over lethal sampling in MPAs are high and the sources of funding for shark telemetry studies generally originate from eco-tourism, analysis of movement is rarely accompanied by lethal sampling. Therefore, the movement behaviour in terms of biology is explained by what is known for that species from other areas or from the same location often decades prior to the study. Life-history of sharks may vary from region to region and as such, interpreting the movement behaviour in terms of incorrect or outdated biology can be misleading. Lethal sampling of sharks is not a requisite for describing their movement. However, the combination of lethal sampling at the same time and space as the movement study is being conducted provides additional information to explain biological motivations underpinning this movement.

CHONDRICHTHYAN MOVEMENT BEHAVIOUR STUDIES

REPRODUCTIVE BEHAVIOUR AND MOVEMENT

Chondrichthyans have evolved independently from teleosts over the last 400 million years (Pough *et al.*, 1999; Sims, 2003). Consequently, they have different morphological

and life-history adaptations which affect their movement. The absence of a gill-plate that can pump water over gills when stationary and the absence of articulated pectoral fins make chondrichthyans, with the exception of those that have spiracles, less likely to adopt station-keeping behaviour and lengthy periods of stasis. Elasmobranchs fall into two categories, those that are able to pump water over their gills through buccal pumping such as elasmobranchs in the Orders Heterodontiformes and Rajiiformes, and ram ventilators where breathing is facilitated by holding the mouth open whilst swimming, like most species in the Orders Myliobatiformes and Carcharhiniformes (Carlson *et al.*, 2004). Buccal pumping sharks in general are less active and demersal. Ram ventilators, on the other hand are generally pelagic and semi-pelagic sharks with increased mobility (Carlson *et al.*, 2004). Certain active species such as lamnid, carcharhinid and sphyrnid sharks are obligate ram ventilators as they are unable to force water over gills when forward movement is slowed or ceased (Carlson *et al.*, 2004). The difference in morphology of the two groups suggests that other general differences in movement patterns may be evident too.

Reproductive behaviour and processes play a large role in the movement of elasmobranchs. These include internal fertilization, multiple paternity, sperm storage, and sex or age-based segregation and dispersal (Klimley, 1987; Economakis and Lobel, 1998; Pardini *et al*., 2001; Sims *et al.*, 2001). Internal fertilization makes reproduction less energetically costly for males (Sims, 2003). Since very little sperm is wasted, minimal energy is required for sperm production as opposed to teleosts which undergo broadcast spawning. Internal fertilization requires males to compete for direct access to females, as insertion of claspers requires that males physically interact with females by restraining them with teeth or body weight.

Multiple paternity is widespread among shark species including *M. mustelus* (Maduna *et al.*, 2018) it has been described in several orders such as Squaliformes (Daly-Engel *et al*., 2010), Carcharhiniformes (Daly-Engel *et al*., 2006), Hexanchifomes (Larson *et al*., 2011), Lamniformes (Gubili *et al*., 2012) and Orectolobiformes (Saville *et al*., 2002). For a species that exhibit philopatry and or have relatively small population size, multiple paternity reduces the likelihood of mating with a genetically incompatible male such as a relative (Chapman *et al*., 2004).

The ability of female sharks to store sperm for several months allows the viable sperm from multiple males to accumulate over a protracted mating season, such as *Prionace glauca* and *S. tiburo* (Pratt 1993, Manire *et al.*, 1995). Storage of sperm likely reduces the energetic costs associated with searching for males (Hussey *et al*., 2010). The period of sperm storage varies among species four weeks in *C. cautus* (White *et al.*, 2002), five months in *G. galeus* (Peres and Vooren, 1991) and 12 months in blue sharks *P. glauca* (Pratt, 1993).

Sized based segregation has been linked to the avoidance of competition for food in *P. glauca* (Queiroz *et al*., 2005; Litvinov, 2006; Montealegre-Quijano and Vooren, 2010), metabolic requirements in *P. glauca* (Queiroz *et al*., 2005), avoidance of predators in *Negaprion brevirostris* (Morrissey and Gruber, 1993a,b; Sundström *et al*., 2001; Digirolamo *et al*., 2012) and cannibalism in *C. leucas* (Simpfendorfer *et al*., 2005a). Males and females may occupy different habitats due to their different nutritional requirements to meet reproductive energy demands (Sims, 2003).

In choosing a habitat, a female shark needs to consider her own resource requirements and the need to increase offspring survival. An area with high prey abundance facilitates feeding; however, when females are likely to cannibalise their young e.g. *C. leucas* they seldom occupy the same habitat (Simpfendorfer *et al.*, 2005). Female and male sharks may also require different habitat requirements as ambient temperature influences metabolic processes (Sims, 2003). Several studies on stingrays and sharks have suggested that females spending time in warmer water have increased embryonic growth and shorter gestation period (Economakis and Lobel 1998, Wallman and Bennet 2006, Mull *et al.*, 2010).

The physical and energetic demands of mating behaviour largely caused by peri-copulatory biting by males are costly (Pratt and Carrier 2001). Sexual harassment by males may drive females to actively avoid aggressive courtship causing refuging behaviour in females (Sims *et al*., 2001, Kimber *et al.*, 2009*)*. For example, female *Scyliorhinus canicula* refuge in shallow water boulder crevices during the day and move into deeper waters to feed at night, as opposed to the alternate pattern in males. These day time habitats provide true refuges from male harassment and copulation since the confinement within the narrow chambers makes copulation physically impossible (Wearmouth *et al*., 2012). Refuging behaviour may reduce foraging excursions if foraging grounds overlap with those of males. Females trade food availability for thermal habitat selection, however in the presence of males, more time was spent in sub-optimal thermal habitats (Sims *et al.*, 2001; Wearmouth *et al*., 2012).

For teleost fish, the study of spatiotemporal behaviour entails the examination of the dispersal of eggs, larvae and the movements of the adult phase (Bone and Moore, 2008).

Elasmobranchs are mostly live bearing but a proportion of families (24%) are oviparous. Eggs are always deposited on the benthos or attached to macrophytes or sessile invertebrates. Consequently, there is no passive egg or larval dispersal phase and the ability to colonise and recolonize areas rests entirely on the movement of the juvenile or mature shark (Bone and Moore 2008). Fish migration is often a mechanism that ensures the deposition of eggs in the correct water mass relying in the water mass for recruitment onto nursery grounds (Harden Jones, 1968). Oviparous elasmobranchs strategically seek out suitable habitat where eggs remain more or less in the same area embedded in the sediment like *Callorhinchus capensis* (Freer and Griffiths, 1993) and *Chiloscyllium punctatum* (Kempster *et al.*, 2013) or firmly attach to suitable hard structure like *Scyliorhinus capensis* (Ebert *et al.*, 2006) and *Apristurus microps* (Ebert *et al*., 2006). Viviparous and oviparous elasmobranchs utilise nursery grounds defined by Heupel *et al.*, (2007) as areas where newborn and young-of-the-year sharks are more abundant than in other areas, tend to spend extended periods and return repeatedly across different years.

As a result of their biology and reproductive modes, elasmobranchs tend to have less surplus production and a lower rate of intrinsic population increase than teleosts. Biological traits such as longevity, slow growth, low natural mortality rate and low fecundity render them more vulnerable to fishing activities (Smith *et al.*¸1998; Stevens *et al*., 2000; Field *et al*., 2009). Crucial life-history stages, such as pupping and mating aggregations, have significant consequences on the spatio-temporal behaviour of sharks (Kohler and Turner, 2001; Dicken *et al.*, 2006; Hussey *et al*., 2009), especially with species that usually segregate by sex and size (Klimley, 1987; Pardini *et al*., 2001). In addition, sex and size biased dispersal and gene flow make them vulnerable to fishing

practices as high concentrations of sharks may be found in small areas. Alternatively, sex and size segregation make particular size or sex species more vulnerable to fishing.

Complex movement behaviour is seldom included in assessment models. Classic stock assessment models assume a single, homogenous space which encompasses the overall stock and fishing effort. An unfortunate consequence is that the spatio-temporal behaviour of fishes and sharks (i.e. the fact that they can cover larger distances) is seldom considered when fisheries management decisions are made (Goethel *et al.*, 2011). This is evident, for example by the management of migrant species such as *P. glauca* by multiple Regional Management Forums (RFMOs) with minimal overlap between neighbouring RFMOs. Such consequences may not be severe when swimming patterns result in random distribution across fishing areas, but this is not seldom the case. For example, *C. capensis* segregates by sex in offshore waters and migrates inshore to breed (Freer and Griffiths, 1993). Consequently, the potential exists for large numbers of *C. capensis* of a given sex to be caught in a single trawl offshore, or for breeding males and females to be caught in inshore gillnet fisheries (Freer and Griffiths, 1993). Evaluating of the effectiveness of spatial protection is complicated by habitats that are not heterogeneous and species distribution is not uniform (Edgar *et al.*, 2014).

DEFINING MOVEMENT AND MIGRATION

The main advantage of residency is familiarity with the surrounding areas, which facilitates optimisation of foraging and predator avoidance (Jonsson and Jonsson, 1993). However, prey availability and presence of predators vary with environmental conditions (Dingle, 1996; Dingle and Drake 2007). The cost of leaving a familiar area must be balanced by perceived benefits of moving to an unfamiliar or new area (Dingle, 1996;

Dingle and Drake 2007; Jonsson and Jonsson, 1993). Therefore, migration can be seen as a way to adapt to habitats where resource availability fluctuates and where threats in the form of parasites or predators may appear (Chapman *et al*., 2012).

Movement behaviour can be classified according to time (i.e. seasonal), direction (i.e. horizontal, vertical), magnitude (i.e. sedentary, trans-oceanic), or purpose (i.e. spawning migration) (Fréon *et al*., 2010). Movement behaviour of fishes may be driven by the daily activity cycle, such as predator avoidance, foraging and resting and adjustments to changing environmental conditions. In coastal regions, the latter could be influenced by short to medium cycles related to tide, or photoperiod. On a longer temporal scale, movements can be related to seasonal changes in the environment or coupled with the reproductive cycle.

For the purpose of this study migration is defined according to Dingle's (1996) definition modified from Kennedy 's (1985) "Migratory behaviour is persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle". Migration is widespread among vertebrates, in particular birds (Newton, 2008), mammals (Sanderson, 1966), reptiles (Southwood and Avens, 2010) and amphibians (Adams and Frissell, 2001; Santos and Grant, 2011) fish (Fréon *et al*., 2010) and sharks (Sundström *et al*., 2001). Not all individuals within a population migrate, even amongst classic migrants such as salmon (Hendry, 2004) and migratory swallows (Southern, 1938; Alerstam, 1990; Newton, 2008). There is a large degree of variation in what occurs amongst individuals or between discrete groups within a population (Nathan *et al.*, 2008, Fréon *et al.*, 2010). This phenomenon known as partial

migration, first described by Lack (1944), has been documented in *Galeocerdo cuvier* (Papastamatiou *et al.*, 2013a,b) but is expected to be more widespread in sharks.

METHODS OF STUDYING FISH AND SHARK MOVEMENT

Elasmobranch tagging began in 1936 when skates and rays were tagged around the British Isles (Kohler and Turner, 2001). The study of movement of aquatic organisms has seen some dramatic improvements through the invention of novel tracking techniques. A comprehensive review of the historical development of external tags and markings was completed by McFarlane *et al.*, (1990). The earliest marking of an animal most likely occurred between 218 and 201 B.C when a swallow marked with a thread knotted to indicate date of a planned relief attack was sent by a besieged garrison (Delany, 1978). Early fish mark-recapture methods relied on the return of external tags from fishermen and provided data on the –tag and recapture events only. Many different types of external tags (e.g. copper chain, celluloid collar and disk, barb, strap, Petersen disk) were developed for different fish, different positions on the fish and different attachment methods (e.g. anchor, umbrella) (McFarlane *et al.*, 1990; Kohler and Turner, 2001). Due to low retention rates and low reporting of recaptured tagged fishes, studies using traditional external methods generally need to be based on large number of individuals to provide information about the movement of fishes (Thorstad *et al*., 2013). The first large-scale tagging programmes on sharks were initiated in the 1940s aimed at dogfish dogfish *Squalus suckleyi* using Petersen disk tags wired through the first dorsal fin. (Foerster, 1942; Bonham *et al*., 1949; Stevens, 1999a). Since the 1990s, traditional tagging mark-recapture studies have been adapted to include photo-identification, a non-invasive approach allowing multiple recaptures unaccompanied by accumulative stress on the study animal (Wiirsig and Jefferson 1990, Slooten *et al.*, 1992, Meekan, 2006).

This method has been used on many species with external markings that vary with individuals including *C. carcharias* (Towner *et al*., 2013), *Cephalorhynchus hectori* (Slooten *et al.*, 1992), turtles (Schofield *et al*., 2008) and manatees (Reid *et al.*, 1991). This method is limited in scale and practicality since multiple photographs of the same animal is required for a positive identification, many fish don't have recognisable identifiable markings and processing time of photographs through photo-identification software is time and computationally intensive.

A detailed review of electronic tags and acoustic telemetry was provided by Thorstad *et al.*, (2013) and Hockersmith and Beeman (2012), and is therefore beyond the scope of this study, except to provide a brief overview for introduction purposes. The recent development of electronic tracking technology (telemetry) since the 1950s has provided the tools to get a fresh look at animal movement behaviour including those of fish. Fish telemetry involves all methods used to obtain information on free-ranging fish at a distance (Thorstad *et al*., 2013). Electronic tagging methods have facilitated the collection of long-term data on the movement, physiology and environmental parameters collected from each fish, depending on the type of tag used (Thorstad *et al*., 2013). Since detailed information can be collected from fish without the help of others returning tag and tag information, this reduced the numbers of fish required to answer research questions. A large variety of electronic tags are now available, including radio transmitters, acoustic transmitters, archival tags and pop-up archival satellite tags.

Radio transmitters, first used in 1956, allow for active tracking of a fish with a portable receiver and aerial antenna or by stationary receivers in fresh water. This method is not feasible in salt or brackish water due to attenuation of radio signals due to dissolved salts

(Trefethen, 1956; Trefethen *et al.*, 1957; Trefethen and Sutherland, 1968; Hockersmith and Beeman, 2012; Thorstad *et al*., 2013). Acoustic telemetry was first used in 1964 to monitor sturgeon migrations (Hockersmith and Beeman 2012). Acoustic telemetry employs manual tracking methods (Hawkins *et al*., 1974) or fixed acoustic arrays (Heupel *et al.*, 2006). Manual tracking methods utilises a portable receiver and antennae, generally from a boat since the hydrophone needs to be submerged (Thorstad *et al*., 2013). Manual tracking is suitable for the collection of short term data, since data collection is labour intensive. Fixed acoustic arrays for passive tracking use a logger/ listening station to collect information about fish identification and time or sensor data when sensor tags are used to collect environmental data. This method is more suitable for collection of long-term movement data; however, the data collected is limited in quality by the number of receivers per area covered in the study site and the position of the fish is not known but is within the detection range of the receiver where it was recorded.

PSAT (pop-up satellite archival tags) was first used in 1996 on *Thunnus thynnus thynnus* (Block *et al*., 1998). Satellite tags are externally attached to fish and are released at a pre-programmed time aided by a corrosive link. Once released, they float to the surface and transmit data continuously to ARGOS satellites. PSAT are used on large migrant species and use light data which estimates geographic position based on day length variation with latitude and local noon or midnight time variations with longitude (Thorstad *et al*., 2013). Limitations of this use are the cost of PSAT ($499–$4000+) and size of tag which limits the size of the fish studies. Calculating the accuracy of geolocation is complicated by the diving behaviour of fish. The longitudinal positions

are difficult to estimate due to weather and water quality conditions, equinoxes when day lengths are almost equal and polar latitudes (Thorstad *et al.*, 2013).

GLOBAL SHARK TRACKING

Shark tagging studies, including methods, technology and analyses have been comprehensively reviewed (Nelson, 1978; Kohler and Turner, 2001; Sundström *et al*., 2001; Voegeli *et al*., 2001; Sims, 2010; Hammerschlag *et al.*, 2011; Papastamatiou and Lowe, 2012), therefore a thorough review is not necessary here. Tracking studies (Chapman *et al*., 2005; Garla *et al.*, 2006a; Garla *et al*., 2006b) have provided evidence for a degree of site fidelity of juveniles and sub-adult sharks within isolated habitats. For example, juvenile *Carcharhinus melanopterus* prefer shallow sand-flat habitats, while adult sharks can be found on reef ledge habitats (Papastamatiou *et al*., 2009). Many of these studies are based on short term tracking of a small number of individual sharks usually in a single location. Consequently, it is possible that the full range of inter and intra-specific variation are not recorded.

Intra-specific variations in behaviour can be explained on the basis of age and sex (Baker, 1978; Quinn and Brodeur, 1991). However, since many species of sharks are sexually dimorphic (Pratt and Carrier, 2001; Sims, 2005) the largest component of the intra-specific variation in behaviour is a spectrum of behaviours relating to sex such as maturity, conditional movement strategies and actual genetic variation. Intra-specific variations in behaviour may be related to maturity as a consequence of age or size. Juvenile *N. brevirostris* find shelter in mangrove lakes during high tide, providing safe habitat when inshore areas become accessible to predators such as sub-adult *N. brevirostris* (Guttridge *et al*., 2012). Adult sharks will leave the lakes to feed on larger prey and to engage in reproductive behaviour (Guttridge *et al*., 2012).

G. cuvier in Hawaii display conditional movement in which the tactic an individual adopts is determined to some aspect by age, sex and resource (Papastamatiou *et al*., 2013b). To my knowledge there are no studies relating intra-specific variation in movement to genetic variation in sharks, yet this is common in other taxa. Two types of *Orcinus orca* have been described; residents and transients. Resident *O. orca* form larger social groups with smaller area of observation; they have more frequent dive intervals and vocalize more often than transients (Quinn and Brodeur, 1991). Resident *O. orca* eat primarily fish and their movement coincide with the timing and location of salmon migration, whereas transients focus mainly on marine mammals. These two types do not change behaviour nor apparently interbreed; therefore, these differences are likely to be related to genetic differences (Quinn and Brodeur, 1991). These variations in behaviour that increase the likelihood of animals leaving their home range and reproducing at a non-natal location are important from an evolutionary perspective since the behaviour promotes gene flow between populations and the eventual establishment of new populations (Quinn and Brodeur, 1991).

Telemetry studies provide information on the movement behaviour of sharks over time and space but cannot explain why these movements are made. Unusual long-distance movement and sexual or size segregation can frequently be explained by mating and pupping (Pratt and Carrier, 2001; Feldheim *et al.*, 2002; Bonfil *et al*., 2005). *P. glauca* migrate large distances for mating and parturition where large aggregations of mature single sex schools can be found (Pratt and Carrier, 2001). Additionally, the physiological constraints of individual shark and their prey determine the use of space within a habitat (Godin, 1997). As environmental constraints change throughout a shark's life-time these

are likely to affect their habitat requirements. Neonate and young-of-the-year *C. leucas* can often be found in the upper reaches of estuaries, whilst older sharks are found in the lower reaches and adjacent embayments. Although habitat partitioning can be explained by predator avoidance, younger sharks were often found at warmer temperatures (>29 °C) and different salinities than adults (Simpfendorfer *et al*., 2005b). In order to understand why sharks move, it is important to understand their biology and the changing environmental conditions they face over time. Therefore, interactions between life-history, physiology, behaviour and habitat make individual movements an exceptionally complex phenomenon (Patterson *et al*., 2008).

A BRIEF HISTORY OF SHARK TRACKING IN SOUTH AFRICA

In South Africa, acoustic telemetry was first used in 1993 with the monitoring of spawning behaviour of *Loligo vulgaris reynaudii* (Sauer *et al*., 1997; Shabangu *et al*., 2014). The initial study expanded to include the movement squid predators, including *C. taurus* and a number of ray species (Smale *et al*., 2001). These predators are attracted to egg beds and disrupt *L. vulgaris reynaudii* egg laying behaviour. At the instigation of the ecotourism industry, acoustic studies on *C. carcharias* in False Bay commenced in the early 2000s to test the effects of chumming on shark behaviour (Laroche *et al*., 2008). Since then, this study has expanded to investigate shark movements in relation to that of their prey the *Arctocephalus pussilus* (Kock *et al*., 2013).

South African telemetry studies are now designed around arrays of receivers each within one of several bays or estuaries. Major chondrichthyan subjects of study are *C. carcharias* (Kock *et al*., 2013; Towner *et al*., 2013), *C. taurus* (Smale *et al*., 2015), *G. cuvier*, *Notorynchus cepedianus* and *C. leucas* (McCord and Lamberth, 2009). South

African studies have similar limitations as elsewhere; a small number of receivers need to cover a large area due to budget constraints. This limitation is especially pertinent to studies in large bays or open water as opposed to those constrained within small estuaries, lagoons or atolls. Reef habitats and bays are difficult to cover with an adequate number of receivers and therefore arrays are placed in a pattern that maximises the likelihood of detection of tagged individuals.

Some parts of a bay may be of special interest. These might include constrictions or habitat breaks or may be anthropomorphic boundaries such as those that delimit management zones, bathing areas or marine protected areas. At many of these boundaries, it might be important to determine not only the presence of sharks, but also the direction of movement and the frequency of boundary crossings. Array designs will need to be able to provide multiple types of information. Small scale movement behaviour may be difficult to describe where data are limited to presence/ absence data. Information on direction for example could be matched with environmental data to test the effects of atmospheric fronts, tides, intrusions of cold or warm water masses, and the diel cycle on behaviour. South Africa has one of the most diverse chondrichthyan faunas in the world with approximately 204 species from 13 orders (Ebert and van Hees, 2015), approximately 50% of which are caught in 9 of South Africa's 17 commercial fisheries (da Silva *et al.*, 2015). *M. mustelus* represents one of the top five commercially valuable species in South Africa, occurs in high numbers close inshore and is therefore most suited to spatial protection.

MUSTELUS MUSTELUS GLOBALLY AND IN SOUTH AFRICA

Mustelus mustelus, Triakidae is a medium sized demersal shark common in South Africa but also occurs in the eastern Atlantic from the British Isles to South Africa (Compagno, 1984). They are abundant in small enclosed bays with soft substrate (Smale and Compagno, 1997). *M. mustelus* reproduction is placental viviparous (Compagno 1984), with a gestation period of 7-12 months, and litter sizes between one and 25 pups (Capapé *et al*., 1974,Capapé *et al*., 2006, Khallahi 2004, Saïdi *et al*., 2008, Smale and Goosen 1994). Little is known about *M. mustelus* nurseries; however, these are suspected to occur inside sheltered inshore bays (Peters *et al.*, 2000). *M. mustelus* in South Africa are genetically structured into Atlantic and Indian Ocean stocks (Maduna *et al*., 2016; Maduna *et al*., 2017; Maduna, 2017). As the results of the *M. mustelus* genetics study are recent, possible differences in age and growth, reproduction and maturity between populations have not been investigated.

M. mustelus are fished throughout their range (Constantini *et al.*, 2000, da Silva, 2007, Saïdi *et al.*, 2008). In South Africa *M. mustelus* is caught in six of the 17 commercial fisheries (da Silva *et al.*, 2015) with an average annual reported catch of between 284 to 426 t between 2010 and 2012. The commercial linefishery and the demersal shark longline target *M. mustelus*, when teleost catches are poor (da Silva *et al.*, 2015). *M. mustelus* are caught as by-catch in the inshore trawl fishery, hake longline fishery and gill and beach seine net fisheries (da Silva *et al*., 2015). Despite large catches of *M. mustelus* across various fisheries there are few management interventions in place to protect them. No specific permit conditions are currently in place in the commercial linefishery. The demersal shark longline fishery is managed under a Total Allowable Effort (TAE) of six vessels, but no other restrictions exist. As of 2016, the Department

of Agriculture, Forestry and Fisheries (DAFF) has implemented a slot limit of 70 -130 cm for demersal sharks including *M. mustelus* caught in the demersal shark longline and commercial linefishery. On occasion, they are caught in large numbers by the inshore trawl fishery as by-catch and retained. Gill net fisheries are prohibited from retaining elasmobranchs and beach seine fisheries are only allowed to retain sharks in False Bay where sharks were historically fished with this gear.

THESIS AIMS

This thesis examines the life-history and the movement behaviour of *Mustelus mustelus* in and around the Langebaan Lagoon Marine Protected Area (LMPA) (Figure 1.1), from here forth referred to as the closed area. *M. mustelus* was chosen for this study due to its status as one of the top five commercially valuable chondrichthyan species in South Africa and its relative abundance inside several closed areas including the closed area within the Langebaan Marine Protected Area (Figure 1.1). This shark species has been reasonably well studied across its distribution, including South Africa. They are also abundant within the closed area providing adequate opportunity for lethal sampling to supplement the life-history component of the study.

The overarching aim of this thesis is to examine the biological and ecological circumstances under which a closed area could protect a shark from fishing mortality. This requires an understanding of the local ecology of the species such as which life-history stages are present inside the protected area and what are possible drivers of their presence or absence. Information about age and growth, feeding and reproduction of the *M. mustelus* population in the Saldanha bay (Fig. 1.1), which contains the closed area provides cues to gauge its importance for the local population of *M. mustelus*. This

knowledge is required to investigate the extent to which the Langebaan Lagoon Marine closed area can protect to the population in each of its life-stages. Other questions worth answering include how much time individual *M. mustelus* spend inside the closed area, and how often do they cross the boundary to get exposed to fishing. Are there any underlying temporal patterns governing these movements? As they have been shown to be distinct from the southern and eastern Cape Coast *M. mustelus* (Maduna *et al*., 2017), it is important to understand how they move within Saldanha bay, which represents a unique environment along the West coast of South Africa. An understanding of their seasonal movements or migrations is also important.

Sharks were telemetered over a period of two years to determine their movement with regard to the closed area boundary and their presence within the bay. Animals choose their spatio-temporal based on ambient environmental conditions. Information on environmental parameters was collected on different temporal scales and their effect on fine-scale shark movement was examined to investigate the drivers of movement and to relate the observed patterns to ecological processes. An understanding of the biology of the *M. mustelus* population, the broad and fine scale movement patterns and the main underlying drivers provides the context under which an evaluation of Langebaan closed area as a conservation tool for this species and the general applicability of spatial protection measures for similar species can be undertaken.

The life-history of *M. mustelus* in the Langebaan Lagoon Marine Protected area or closed area is examined in detail in Chapter 2 through the collection of *M. mustelus* over a two-year period inside the closed area. The age, growth and maturity was estimated and compared to those from other regions and from a previous study in South Africa.

The reproductive biology of sharks in the closed area is described with the intention of using the reproductive biology to explain the spatio-temporal behaviour. Lastly, the feeding of sharks in the closed area is examined for ontogenetic differences.

Acoustic receivers were moored inside Saldanha Bay in such a configuration that the array would be able to record if telemetered sharks crossed the closed area boundary and the movement directionality. Twenty-four sharks were acoustically tagged which enabled the examination of the spatio-temporal behaviour of sharks in the LMPA, particularly with the intention of determining the effectiveness of this closed area in protecting this and other species of sharks in Chapter 3. This chapter quantified the proportion of time the sharks spend within the confines of the closed area with a view to predicting the degree of protection provided. It was also evaluated whether the movement in and out of the closed is seasonal and predictable in order to evaluate possible consequences of seasonal movement. After addressing the above, I examine the possibility that the closed is a nursery for *M. mustelus* by applying the criteria suggested by Heupel *et al.*, (2007) that neonate and juvenile sharks are more commonly found within the closed area than outside, that they have a tendency to remain inside the closed area for extended periods of time and when they leave they often return, and that the area is repeatedly used across years.

The acoustic array was moored in a linear arrangement within the tidal channels inside Langebaan Lagoon, this was accompanied by the placement of a number of temperature-depth recorders at key points. This linear arrangement, minilog placement and ability to detect movement directionality allowed for fine-scale monitoring of movement in relation to environmental conditions. The environmental conditions experienced within

the closed area and Saldanha Bay surrounds are examined in Chapter 4. The movement behaviour in relation to the environmental conditions, particularly with relation to temperature and tide is investigated in detail. The following hypotheses are examined; movement responses in relation to changing thermal environment are related to thermoregulation and changing thermal environment cause animals to move or expand their habitat. Lastly, this study examines the relationship between tidal fluctuations and spatio-temporal behaviour, particularly if movement is related to tidal cycles and if such movement occurs, whether this is related to the biology of sharks examined in the previous chapter.

The thesis is concluded by a brief synopsis integrating the findings of the three method chapters. Chapter 5 evaluates the spatio-temporal behaviour of *M. mustelus* in terms of their life-history strategies under changing environmental conditions. Lastly this chapter discusses whether my findings might be applicable to other chondrichthyans occurring inside and around closed areas with the intention of providing resource management suggestions.

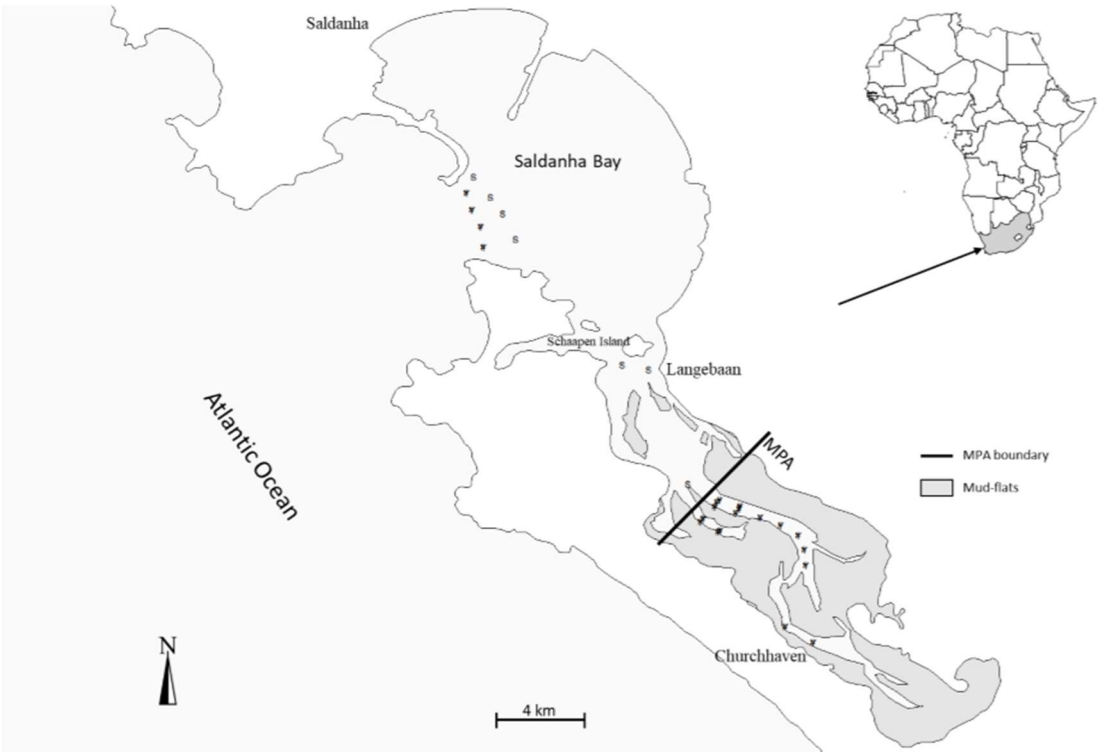


Figure 1.1. Saldanha Bay on the west coast of South Africa and its southern extension, the Langebaan Lagoon, which includes the closed area. The grey shaded area within the closed area boundary represents sandbanks shallower than 2 m deep.

CHAPTER 2: LIFE-HISTORY OF *MUSTELUS MUSTELUS* IN LANGEBAAN LAGOON CLOSED AREA

ABSTRACT

The reproductive biology, diet, growth and maturity of *Mustelus mustelus* was studied in the Saldanha Bay region in the south-western Cape Coast of South Africa between 2007 and 2009. A total of 217 sharks were examined ranging in size from 381 to 1734 mm TL and 467 to 1267 mm TL for females and males, respectively. Sharks in the Bay represented the largest females and males recorded from six studied regions globally. Females are significantly larger than males with an average 220 mm difference. Colour patterning not described before for this species in the form of dark spots was evident in sharks larger than 1000 mm TL.

The seasonal changes in oocytes and testes development, embryo length and the occurrence of near-term and post-partum females indicated that female parturition occurred between November and December after a gestation period of 10-11 months. Ovulation and mating occurs during the same period. The embryo sex ratio was not significantly different from unity. Uterine fecundity increased with the size of mother and larger mothers gave birth to larger pups. This study was unable to confirm the reproductive periodicity found elsewhere. The presence of neonates, juveniles as well as pregnant females inside the LMPA and their absence outside indicates that it may be a nursery ground for this species. The confirmation of the geographical extent of nurseries is vital for conservation plans.

The diet of *M. mustelus* in the lagoon consisted of predominantly three species of crustaceans; *Hymenosoma orbiculare*, *Upogebia africana* and *Callichirus kraussi*. No

ontogenetic shift in diet was observed for *M. mustelus* from Saldanha Bay, contrary to findings elsewhere in South Africa.

This study also investigated the growth rates of *M. mustelus* caught in Langebaan Lagoon through an analysis of growth increments in vertebral centra. The von Bertalanffy growth parameters for the combined sexes illustrate that a maximum asymptotic total length (L_∞) of 1594 mm TL, with a Brody's growth coefficient (K) of 0.15 year^{-1}, and an age at zero length (t_0) of -2.01 (n = 95). Female *M. mustelus* attain a L_∞ of 1898 mm TL, with a K of 0.11 year^{-1} and a t_0 of -2.08 (n = 53). Male *M. mustelus* reach an L_∞ of 1120 mm TL, a K of 0.41 and a t_0 of -1.26 (n = 42). A significant difference in growth between sexes was observed (x^2 = 22.67, DF = 3, $p < 0.05$). A maximum age of 13 for combined sexes was observed in this study, almost half of what was described previously but closer to what has been found for other *Mustelids*. Micro-computed tomography was investigated as an alternative aging method. Age estimates from generated virtual sections *in lieu* of vertebral sections, density calibration plots and virtual sections and density calibration plots combined were compared. The use of micro-computed tomography highlighted the existence of "false" bands responsible for overinflating previous age estimates. L_{50} was estimated at 1194 mm TL and 967 mm TL, corresponding to an age of 6.2 years and 3.1 years for females and males, respectively. A significant difference in length at 50 % maturity between females and males was evident (x^2 = 45.46, DF = 3, $p < 0.001$).

The results of this study indicated that several crucial life-history stages of *M. mustelus* occurred within the Langebaan Lagoon MPA hereafter referred to as closed area including pupping grounds, nursery grounds and feeding grounds at all sizes. Therefore, if sharks spent a large portion of their time or aggregate inside the closed area they would be protected

during these key life-history events or phases. The movement of *M. mustelus* in and around the closed area during these crucial life-history stages would significantly affect the protection provided by the closed area. A thorough understanding of the biology of *M. mustelus* is a precursor to an understanding of the motivations behind spatio-temporal behaviour.

INTRODUCTION

Triakid sharks of the genus *Mustelus* (Linck, 1790) are common over the continental shelves in tropical and temperate waters worldwide (Compagno, 1984; Saïdi *et al*., 2008; da Silva and McCord, 2013). *Mustelus mustelus* occurs in the Mediterranean Sea and eastern Atlantic from the British Isles to South Africa (Compagno, 1984; Saïdi *et al*., 2008; da Silva and McCord, 2013). *M. mustelus* are slender medium sized strong-swimming, benthic feeders with flattened ventral surfaces on the head and body (Smith and Heemstra, 1986). These sharks have small pavement teeth in multi-serial rows that are adapted for preying on hard shelled slow-moving invertebrates. Typical prey items include gastropods, bivalves, cephalopods, echiurids, sipunculids, annelid worms, tunicates, various species of teleosts, and carrion (Compagno, 1984).

In South Africa *Mustelus mustelus* are abundant in enclosed bays with soft substrate (Smale and Compagno, 1997). Although there is considerable overlap in depth preference between sex and age classes, mature and pregnant females frequent shallower depths than immature females and males (Smale and Compagno, 1997).

M. mustelus, like many other Triakid sharks, have a placental viviparous reproduction mode. Their growth, maturity and reproduction have been studied throughout their range: Senegal (Capapé *et al*., 2006), Mauritania (Khallahi, 2004), Gulf of Tunis (Capapé, 1974), Gulf of Gabés (Saïdi *et al*., 2009) and South Africa (Smale and Compagno, 1997; da Silva, 2007). Global maximum lengths of *Mustelus mustelus* range between 900 - 1450 mm TL and 1100-1650 mm TL for males and females, respectively. Maximum recorded ages for *M. mustelus* have been estimated as 25 years by Smale and Compagno (1997) and da Silva (2007) in South Africa. Elsewhere, the maximum age of *M. mustelus* has not been established.

However, maximum recorded ages for the genus *Mustelus* are seldom over 16 years. *Mustelus antarcticus* reaches a maximum age at 16+ years (Moulton *et al*., *1992*), *M. manazo* 9+ (Tanaka and Mizue, 1979) and *M. californicus* 9+ (Yudin *et al*.,*1990*).

Length 50 % maturity (L_{50}) has been estimated at between 570 and 1100 mm TL and 590 and 1400 mm TL for males and females, respectively (Capapé, 1974; Smale and Compagno, 1997; Khallahi, 2004; Capapé *et al*., 2006; da Silva, 2007; Saïdi *et al.*, 2008). Size at birth ranges from 240-450 mm TL, litter size ranges from 1 to 23 and gestation period ranges from 7 to12 months. The lowest gestation estimates came from studies conducted in Mauritania (Khallahi, 2004), while the highest originated from studies from South Africa (Smale and Compagno, 1997). Little is known about the nursery areas for *M. mustelus*, however these are suspected to occur inside sheltered inshore bays (Peters *et al*., 2000).

M. mustelus are exploited throughout their range (Constantini *et al.*, 2000; da Silva, 2007; Saïdi *et al.*, 2008; da Silva *et al.*, 2015). The analysis of biological data, including the estimation of growth, maturity, reproductive seasonality and natural mortality, provide the foundation for quantitative stock assessments (Kanyerere *et al*., 2005). Stock assessments guide fisheries management policies by providing stock status, biological reference points and catch limits (Beamish and Fournier, 1981; Officer *et al.*, 1996; Campana, 2001; Passerotti *et al.*, 2014).

M. mustelus is common on the South African West Coast, and particularly around Langebaan Lagoon (da Silva and McCord, 2013). The closed area within the warm, sheltered, shallow Langebaan Marine Protected Area provides a unique habitat for *M. mustelus*. Personal observations on the size, girth and presence of a large degree of body patterning suggests a

difference between the *M. mustelus* between the Langebaan Lagoon and other regions. This was expected given the genetic structuring provided by the Atlantic and Indian Ocean boundary (Maduna *et al*., 2017). Differences in life-history parameters of populations residing in Langebaan Lagoon and other areas have been found for a number of fish species. *Spondyliosoma emarginatum* grow faster and are larger in Langebaan Lagoon than elsewhere (Tunley *et al*., 2009), similarly, size at 50 % maturity and growth of *Rhabdosargus globiceps* are larger for the South-Western Cape which includes the Langebaan Lagoon and Saldanha Bay (Griffiths *et al*., 2002). It is therefore likely that the life-history of *M. mustelus* from this area is not adequately represented by samples collected in other regions and that Saldanha Bay sharks will exhibit measurable biological differences from other populations. The findings will then be compared to observations from other studies, to determine if life-history and feeding habit in Langebaan Lagoon differs from what has been observed elsewhere. This information will be used to interpret movement behaviour described in later chapters. Lastly, the findings will be used to predict which life-history parameters would influence the protection of a coastal shark population within a closed area.

MATERIALS AND METHODS

Sampling and general methods

M. mustelus were sampled from the Langebaan Lagoon between 2007 and 2009 inside the Langebaan Lagoon closed area (Fig. 2.1). As sampling was undertaken from a small boat only small numbers of sharks could be collected at a time. Sampling undertaken in Langebaan Lagoon aimed to collect 30 sharks a month with no more than 2 sharks from each size category (< 400, 401-600, 601-800,801-1000, 1001-1200, 1201-1400 and < 1400 mm TL). The sharks were caught using rod and reel using squid as bait under a Department of

Agriculture, Forestry and Fisheries Research permit. Individuals were sexed and measured to the nearest mm and weighed to the nearest 1 g. A total of 217 *M. mustelus* were examined in this study. Data collected through standardized angling surveys conducted at field camps by the Zoology Department at University of Cape Town (UCT) between 2004 and 2015. A total of 185 *M. mustelus* were caught inside the closed area. Only eight of these were caught outside the LMPA over the sampling period.

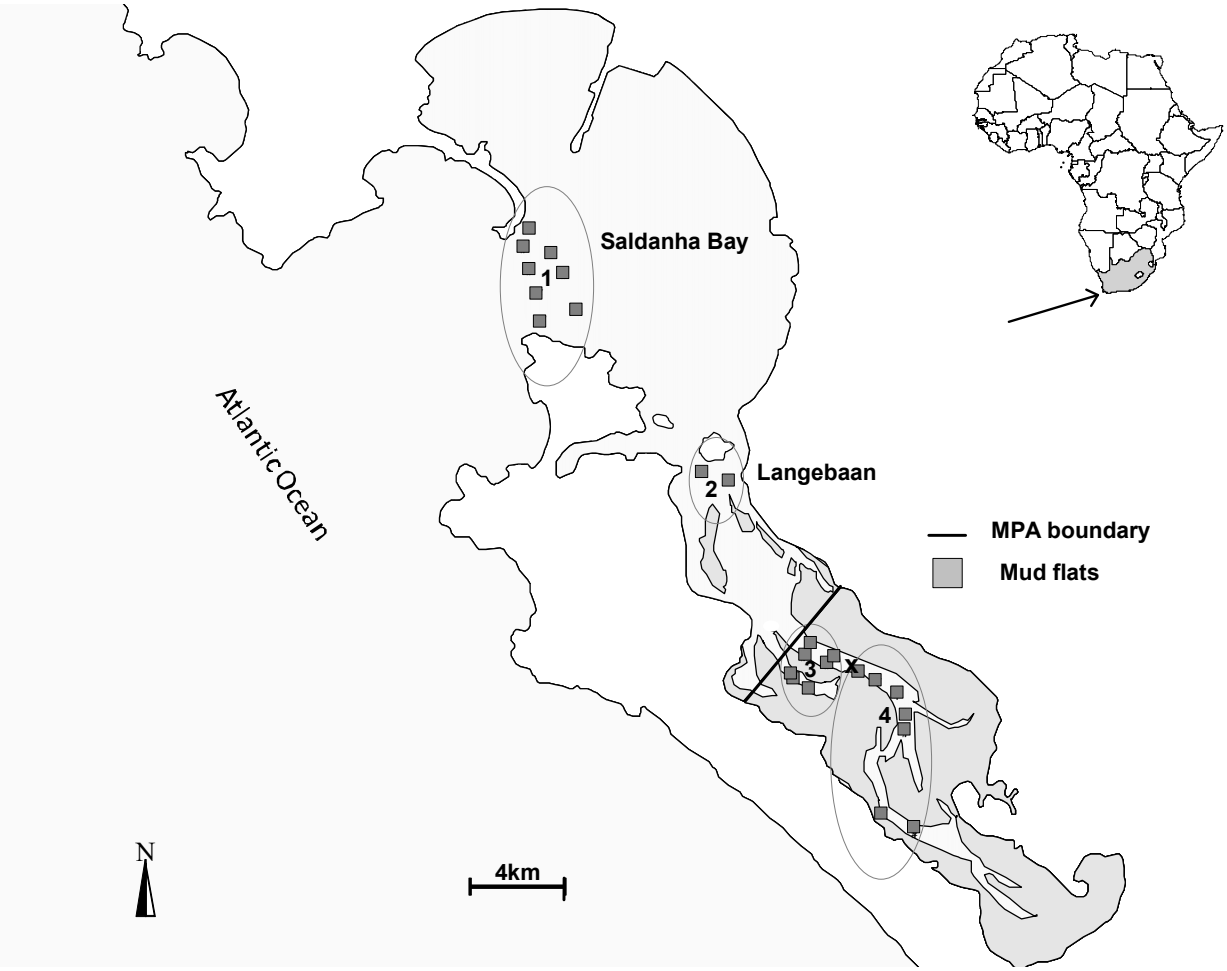


Figure 2.1. Saldanha Bay on the west coast of South Africa and its southern extension, the Langebaan Lagoon, which includes the MPA (closed area). Small grey squares denote individual receiver positions within the four receiver areas (1-4, indicated by grey circles). The grey shaded area within the closed area boundary represents sandbanks shallower than 2 m deep. Catch and release position are denoted by x.

The length–weight relationship was calculated using the least squares fitting method to estimate the two parameters of the function

$$ln(W) = ln(a) + ln(TL)b \quad [1]$$

after W and TL were log-transformed. The linear regression using data from male was compared to that of the female using analysis of co-variance (ANCOVA) to determine if the relationship differed between sexes.

A wide range of patterning was visible on the bodies of the sampled sharks, from no patterning to a large proportion of the body covered in black spots. The percentage of the body covered by black markings was estimated visually for each individual (*percentage body patterning (% BP)*). Chi-squared tests from contingency tables were used to determine if the differences in the presence of BP was influenced by size, sex or maturity separately.

Reproductive biology of *M. mustelus*

Females

Maturity was assessed on the condition of the uteri. Females were grouped under the following categories: immature (thin, thread-like uteri firmly attached to the dorsal wall of the body cavity and an ovary with indistinguishable ovarian follicles), maturing (widening uteri, enlarged ovaries and white ovarian follicles of various sizes), mature (widened uteri with or without visible eggs or embryos and vitellogenic ovarian follicles), using modified criteria of Bass *et al.*, (1975) and Smale and Compagno (1997). Developing oocytes bigger than 0.5 mm in diameter were counted.

The uteri of the pregnant sharks were opened and the number of ova and embryos, and the embryo length and sex (where evident) were recorded. Embryos were classified with the following stages developed for the purpose of this study a) developing yolk sack with embryo small or barely visible embryo, b) vitillin cord formed separating the yolk sack and embryo, c) yolk sack larger or similar size as embryo - gill emersion started, d) embryo larger than yolk sack, placental attachment formed, e) fully formed shark. Scarring inside the uterus of a mature female was taken as an indication of parturition. Uterine fecundity was determined as the number of embryos within the uteri plus the number of *vitellogenic oocytes*, while the number of vitellogenic oocytes determined the ovarian fecundity. The occurrence of ovulation was noted.

The Gonadosomatic Index (GSI) is an indicator of the female reproductive cycle and was determined as follows:

$$\text{Female GSI} = 100\ (\text{Ovary mass}) \times (\text{Total mass})^{-1} \quad [2]$$

Generalized Linear Models were used to investigate the differences between the predictor variables *female size* (mm TL), while controlling for *season* and the response variables *number of vitellogenic oocytes OV*, *litter size* and *ovarian fecundity* (combined number of vitellogenic oocytes and pups), and *pup size* (mm TL), respectively. The continuous response *pup size* was fitted, assuming a normal distribution, which indicated no violations upon inspection of residuals. Because the three other response variables represented counts with occasional large values, a negative Binomial was assumed to account for resulting overdispersion (i.e. variance > mean). Selection of models was conducted considering parsimony using Akaike's Information Criterion (AIC).

Males

Male maturity level was determined using the criteria modified from Saïdi et al (2008) and Smale and Compagno (1997): immature (short, soft claspers, thread-like testes and straight ductus deferens), maturing (partially calcified claspers extending beyond the fins, thickened testes, coiling ductus deferens), mature (fully calcified claspers, enlarged structured testes, and tightly coiled ductus deferens), using modified criteria of Bass *et al.*, (1975) and Smale and Compagno (1997). The presence of sperm in the sperm gland was also noted but was only used as a secondary indication of maturity. The outer clasper length (OCL) was measured as the distance from the tip to the pelvic girdle, and inner clasper (ICL) length was measured as the distance from the tip to the cloacal opening. For each reproductive tract, the condition of the epididymis and the ductus deferens was noted. The testes were removed from the surrounding epigonal organ and weighed to the nearest 0.1 g. The GSI is an indicator of the male reproductive cycle and was determined as follows:

$$Male\ GSI = 100\ x\ (Testes\ mass)\ x\ (Total\ mass)^{-1}. \quad [3]$$

Diet of *M. mustelus*

The stomach contents of dissected sharks were examined and prey identified to the lowest possible taxonomic level. Since the feeding habits of *M. mustelus* were examined in detail by Smale and Compagno (1997), prey items were counted not weighed and their frequency of occurrence (as a percentage of examined stomach was calculated). To analyse the diet composition of sharks relative to size, sex and maturity and to compare with results from Saïdi et *al.,* (2009) and Smale and Compagno (1997), five size classes were identified: newborn (<500 mm TL), young (between 500 and 700 mm TL), small (between 700 and 900 mm TL), medium (between 900 and 1100 mm TL) and large (>1100 mm). Effects of size, sex and maturity on prey selection was tested using analysis of similarities (ANOSIM) in "R"

(R development Core Team 2008; http:///CRAN.R-project.org/), dissimilarity indices was computed and implemented with the Bray-Curtis method with the Vegan package (http://cran.rproject.org/web/packages/vegan/index.html). If relationships were significant, similarity percentage analysis (SIMPER) using the Vegan package in "R" was used to determine the percentage contribution.

Growth of *M. mustelus*

Preparation of vertebrae

Protocol for preparing vertebral sections for aging was modified using a combination of methods by Goosen and Smale (1997) and Bennet (2004). Five of the largest vertebrae were removed from the vertebral column below the first dorsal fin. The neural and haemal arches were removed from two of the five vertebrae and all five were then refrozen for storage and later processing. The centra were then submerged in boiling water for two to five minutes and soaked in a 4.5 % solution of sodium hypochlorite for 14-45 minutes to remove excess connective tissue depending on the size of the vertebrae (larger vertebrae soaked for longer periods). Centra were resin-embedded and sectioned.

A section at the widest diameter of each vertebra was cut sagittally, with an otolith saw fitted with two Leco diamond blades (Size 5" x .025 X1/2") to a thickness of approximately 0.3 mm. Sections were stained with an Alizarin red S stain prepared by mixing the supernatant of a saturated aqueous solution of Alizarin red with 0.1 % NaOh in a 1:18 ratio. Each section was stained for two minutes, washed in tap water for ten minutes, soaked in 3 % H_20_2 for one hour and then rinsed in tap water. Sections were mounted on glass slides with D.P.X. mountant (Qualigens fine chemicals) and viewed at a set magnification (10 X) using transmitted light. The number of growth bands was taken as the age estimate, each growth zone consisting of one translucent and one opaque band. Since no suitable recaptured sharks

injected with oxytetracycline was available, no age validation was done and readings were treated as age estimates (Figure 2.2).

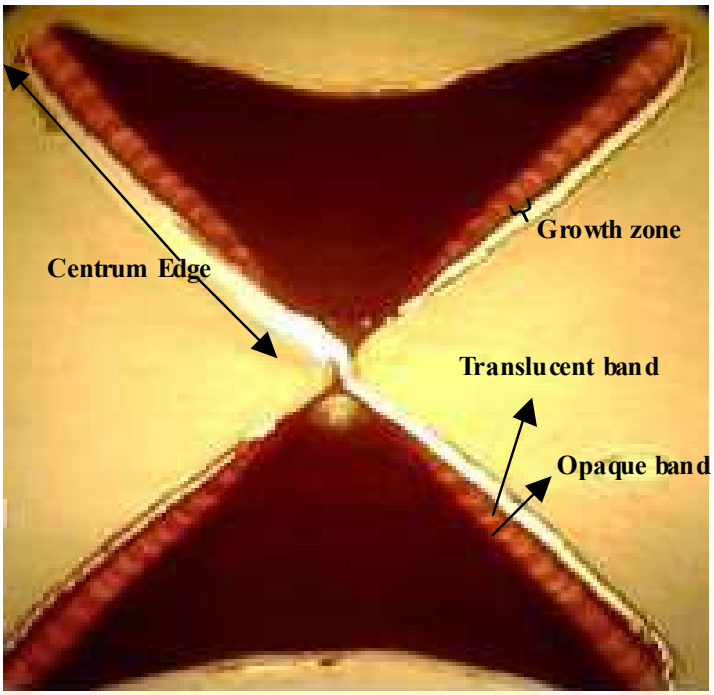


Figure 2.2 Vertebra from *M. mustelus* stained with Alizarin red for enhanced quality (Bennett, 2004).

Growth patterns

As this study was an extension of previous studies by Goosen and Smale (1997), Bennett (2004) and da Silva (2007). Growth curves were fitted to observed data using a von Bertalanffy growth function.

Total length as a function of age t is modelled as

$$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right) \qquad [4]$$

where L_∞ is the maximum theoretical length, k is the rate at which L_∞ is reached, and t_o the theoretical age at zero length. As there was less variation in length-at-age in younger sharks than older ones, a log-normal error structure was assumed. Parameter estimates were obtained using non-linear minimisation of a negative log-likelihood function of the form

$$-lnL = \frac{n}{2} ln\left(\frac{\sum_{i=1}^{n}((\ln(L_i) - ln(\hat{L_i}))^2)}{n}\right) + \frac{n}{2} \quad [5]$$

where L_i and $\hat{L}_t$re the observed and model predicted lengths at age, and n the sample size.

A Likelihood Ratio Test (LRT) was also applied to determine whether there was a difference in growth between the sexes. The process can be described as follows: the negative log likelihood of the model fit was calculated for males and females separately yielding sex-specific estimates of L_∞, k and t_o. The full model was compared to a reduced model with combined estimates for females and males. The likelihood ratio was assumed to follow a x^2 distribution and was calculated from the negated Log Likelihoods of the full and reduced models, such that:

$$x_p^2 = 2 \times (-lnL_{Full} - lnL_{Red}) \quad [6]$$

where p denotes the difference between the number of parameters (p = 3) estimated for the full and reduced model.

Parameter variability was calculated through the generation of 1000 independent parametric bootstrap samples drawn randomly with replacement by taking n values of the original sample size. 95 % Confidence intervals were estimated from the bootstrap results by using the percentile method (Buckland, 1984).

Precision Analysis

The occurrence of numerous false translucent and opaque bands complicated the initial reading of vertebral increments. A new set of criteria were developed to identify true growth rings. A set of translucent and opaque bands were only considered a growth increment if the following criteria were met: 1) clearly defined set of translucent and opaque bands, 2) grouping of translucent and opaque bands when clear notches are seen where the intermediala and corpus calcareum meet, 3) grouping is confirmed when a translucent band extends into

the intermediala. Three independent readers made randomized blind counts of translucent and opaque bands in the centra. Count reproducibility was then assessed using the Average Percentage Error (APE) as described by Beamish and Fournier (1981).

$$APE = 100 \times \frac{1}{R} \times \sum_{i=1}^{R} \frac{\left| X_{ij} - X_j \right|}{X_j} \quad [7]$$

X_{ij} represented the i^{th} count for the j^{th} fish, X_j was the average count for the j^{th} fish, and R was the number of counts for each fish.

This method provides error estimates for individual fish while considering the lifespan of the species by considering increased error with larger sizes. An APE limit of 20 % per vertebra, as used by Wintner and Cliff (1995), was set. Samples exceeding this limit were discarded. The final reading excluded discarded samples and, the average of the three counts was used as an age estimate.

The index of average percentage error (APE index) was calculated, according to the following:

$$IAPE = \frac{1}{N} \sum_{j=1}^{N} \left[\frac{1}{R} \times \sum_{i=j}^{R} \frac{\left| X_{ij} - X_j \right|}{X_j} \right] \quad [8]$$

where N is the number of vertebrae with acceptable readability scores (i.e. an APE of less than 20 %). The level of bias was assessed with a linear regression to test an assumption of a 1:1 relationship between readers and if the slope and the intercept were significantly different from one and zero, respectively (Weyl and Booth, 2008).

Alternative aging method: micro-computed tomography (microCT)

As initial readings of vertebral increments yielded high errors due to multiple "false" bands an alternative aging method was investigated. Single vertebrae from each of six randomly selected sharks were scanned with a General Electrical Phoenix V|Tome|X L240 / NF180 micro-tomography system. To provide some phase enhancement to the resulting tomographic projections, the source and x 0.5 scintillator or objective were set at 150 and 200 mm from the vertebra, respectively. The data visualization software myVGL (http://www.volumegraphics.com/en/products/myvgl/) was used to visualize the axial slice stacks in full 3D context. The software permitted complete 3D visualization and facilitated extraction of virtual sections at any orientation through the specimen using digital clipping planes. For quantitative ageing assessment, virtual sections clipped along the sagittal plain were extracted from the six selected vertebrae. Absolute density calibration was done across the centrum edge (Figure 2.2) providing full 3D values for density in g/cm^3. The raw density calibration data was smoothed using a smoothing spline in *r* various degrees of freedom and was used until a suitable smoothing value was found (DF = 100). The virtual vertebrae (VS) sections, density calibration plots (DCP) and combined VS and DCP where read independently by two readers without prior experience in aging sharks. Precision analysis was calculated as above and used as an indication of which method provided more accurate estimates. Age estimates were averaged across method to test reading bias between readers. The level of bias was assessed with a linear regression to test an assumption of a 1:1 relationship between readers and if the slope and the intercept were significantly different from one and zero, respectively (Weyl and Booth, 2008).

Length-at-maturity

The approaches used by Goosen and Smale (1997) and Saïdi *et al*., (2009) were used to determine the length at maturity of female and male *M. mustelus*. Maturity levels as a function of length were modelled by the logistic function:

$$P_l = \left(1 + e^{-(l-l_{50})/\delta}\right)^{-1} \quad [9]$$

where P_l is the proportion of fish mature at length l, l_{50} is the length at which 50 % of the animals are mature, and δ is the inverse rate at which animals mature.

Length ogive parameters were estimated by minimizing the negative ln-likelihood, calculated using the binomial function:

$$-\ln L = -\left(\sum_m y_i \ln\left(\frac{\hat{p}_i}{1-\hat{p}_i}\right) + m_i \ln(1-\hat{p}_i) + \ln\binom{m_i}{y_i}\right) \quad [10]$$

Where m_i is the number of fish sampled in length i, y_i is the number of mature fish in class i and $\hat{p}_i$ the logistic model predicted proportion of fish mature in class i.

A Likelihood Ratio Test (Cerrato, 1990) was conducted to test the null hypothesis that there is no difference between size at maturity for females and males. The process can be described as follows: a negative log likelihood (-*lnL*, equation 5) of the model fit was calculated for males and females separately yielding sex-specific estimates of L_{50} and *delta.* The likelihood ratio was assumed to follow a x^2distribution and was calculated from the negated Log Likelihoods of the full and reduced models (x_p^2 equation 6).

RESULTS

Sample sizes, morphometrics and pigmentation

A total of 217 *M. mustelus* were examined. The females (n = 124) ranged from 381 to 1734 mm TL and the males (n = 93) ranged from 464 to 1267 mm TL (Figure 2.3). Male and female sharks were sampled in every season (Table 2.1). The majority of sharks were caught in autumn (n = 108), followed by spring (n = 60), summer (n = 34) and winter (n = 15).

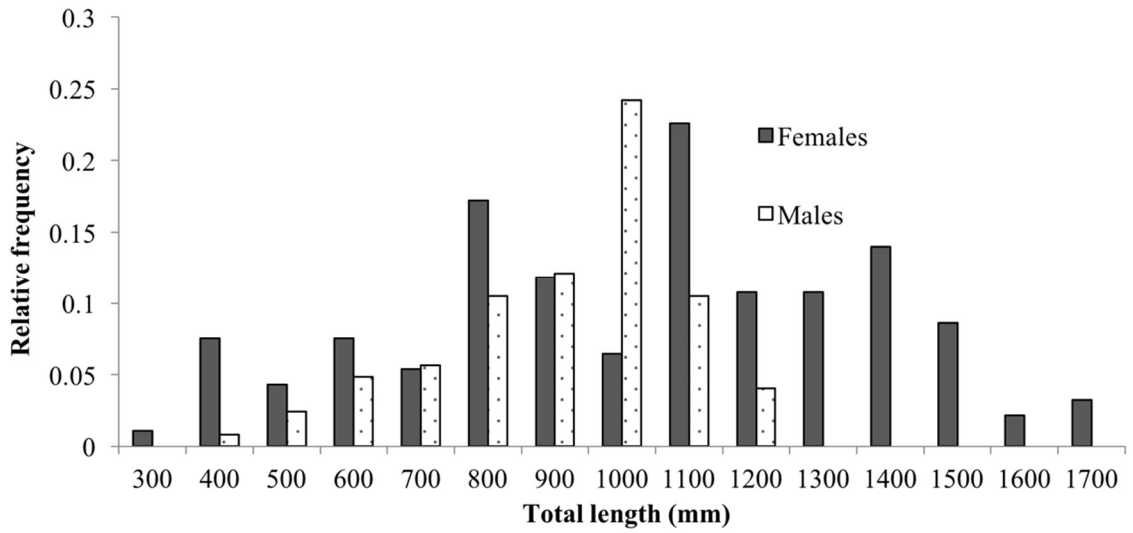


Figure 2.3 Size frequency distribution of *M. mustelus* sampled from Langebaan Lagoon (2007 to 2009) (n=217).

The weight of females ranged from 176 to 2490 g, and the weight of males ranged from 299 to 7385 g. There was no significant difference in shape between males and females (ANCOVA, n = 217, F = 1.75, p = 0.18).

The fitted length weight model for females was $W(g) = 0.000000509\ TL\ (mm)^{3.325}$ $R^2 = 0.98$, and the relationship for males was described by $W(g) = 0.00000081\ TL(mm)^{3.21}$. $R^2 = 0.93$.

Table 2.1. Sample size of *M. mustelus* in Langebaan Lagoon by season between 2007 and 2009.

	Female	Male
Summer	22	12
Autumn	59	49
Winter	8	7
Spring	35	25
Total	124	93

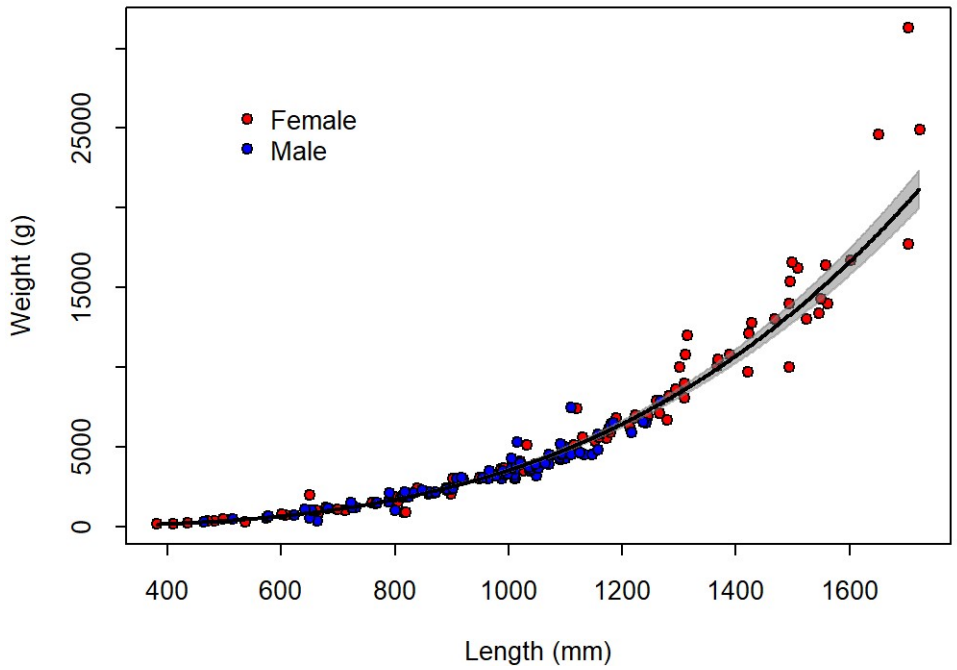


Figure 2.4 Relationship between weight (g) and total length (mm) of male and female *M. mustelus* from Langebaan Lagoon (2007 to 2009).

A total of 180 *M. mustelus* between 360 and 1680 mm TL were caught during sampling surveys undertaking by the University of Cape Town. Sex was only recorded in recent years. Females (n=39) ranged between 360 and 1680 mm TL and male (n=23) ranged between 420 and 1515 mm TL (Figure 2.5), the remaining sharks were unsexed (n=110). Only eight sharks were caught outside the LMPA. The sex ratio between males and females was 0.59:1.

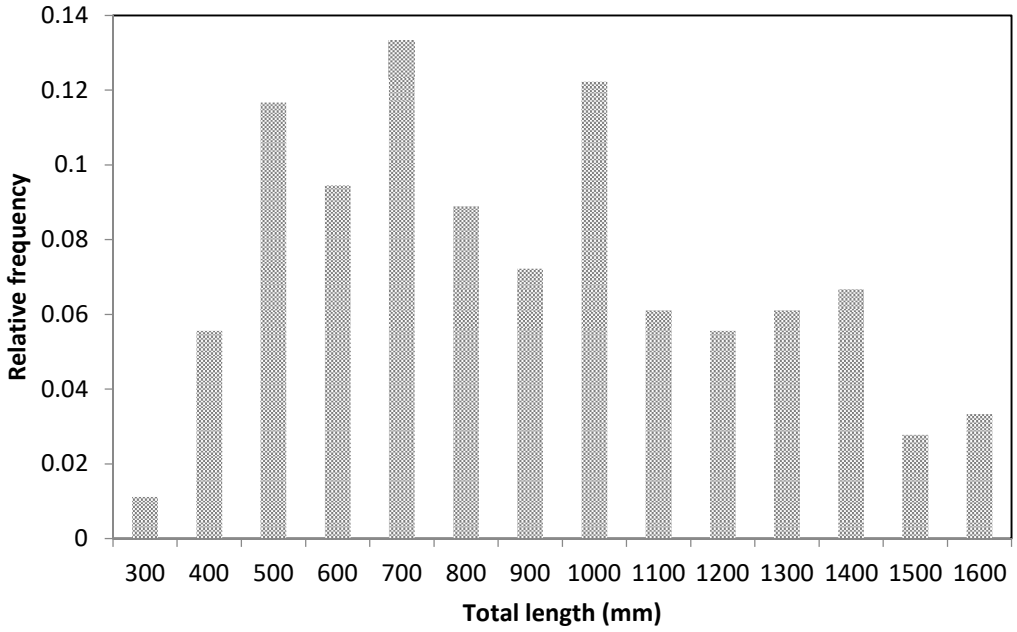


Figure 2.5 Size frequency distribution of *M. mustelus* caught during UCT surveys in the Langebaan Lagoon closed area (2004 to 2015) (n=180).

Body patterning (BP) in the form of different sized black spots was observed on 57 females and 54 males. 65 Females and 39 males had no spots. No BP was exhibited in sharks smaller than 500 mm, while only infrequent BP (14.3 %) was observed in sharks between 500 and 600 mm. Sharks with BP larger than 1000 mm were covered with spots across more than 15 % of their body. The incidence of BP differed between immature and mature sharks (chi-squared test, $\chi^2 = 16.6$, DF = 1, $p < 0.05$), but not between males and females (chi-squared test, $\chi^2 = 0.58$, DF = 1, $p = 0.90$).

Reproductive biology of *M. mustelus*

Females

Description of the reproductive biology

The ovaries of *M. mustelus* are membranous, i.e. the oocytes are held together by a membrane. At the onset of maturity, the shape of the reproductive tract changes. The oviducal glands increase in size and complexity, the uterus thickens posteriorly and the right ovary enlarges (Figure 2.6).

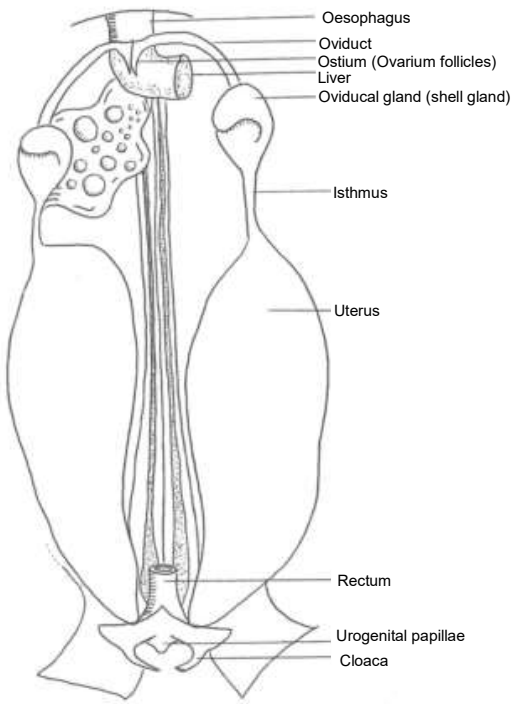


Figure 2.6. The reproductive tract of a mature female *M. mustelus*.

On average, the mature female GSI was 0.5 % (SD = 0.5 %, range 0.1-2.3 %). The average GSI of mature females increased from winter at a value of 0.1 % (SD = 0.1 %, range 0.1- 0.2 %) to summer at a value of 0.9 % (SD = 0.8, range 0.4 - 2.2 %). Despite this difference, there

was no significant seasonal difference in the GSI of mature females (Kruskall Wallis, $x^2 = 8$, DF = 8, p value = 0.43) (Fig. 2.7).

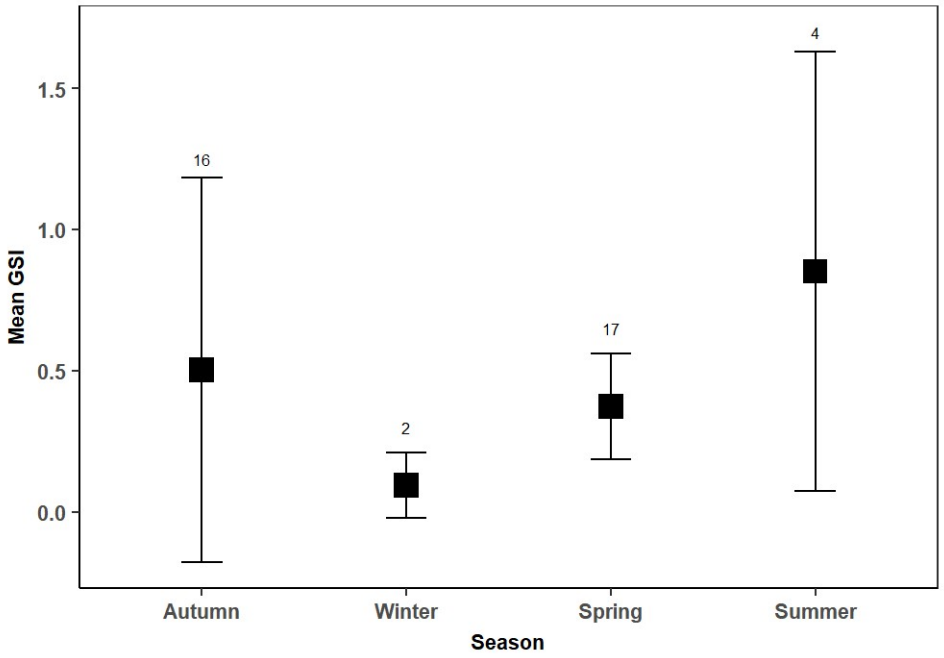


Figure 2.7 Mean ±Standard error gonado-somatic index (GSI) by season for female *Mustelus mustelus*, caught in Langebaan Lagoon. Sample numbers per month are indicated above the error bars.

Mating, embryonic development, gestation, pupping and size at birth

Distinct seasonality was observed in embryo development phase. Embryos were characterized into five developmental phases. Embryos observed between September and December were typically small and barely visible, with a large yolk sack. Embryos observed in February typically had yolk sacks larger or similar in size to the embryos, and showed signs of gill emersion. Embryos observed between April and August were typically larger than the yolk sack and with placental attachment. Embryos observed in September were fully formed neonates.

The *number of vitellogenic oocytes* in mature female *M. mustelus* ranged from 0 to 50 (mean = 15.04, SD = 13.11). There was no relationship between *female size* mm TL and the *number*

of vitellogenic oocytes (n = 49, p =0.06, R^2 = 0.07). The best fit was provided with a negative binomial model.

Litter size ranged from 2 to 26 (mean = 13.68, SD = 6.86). There was no relationship between *female size* mm TL and the *litter size* (Linear Regression, n = 19, R^2 = 0.12, p = 0.15). The best fit was provided with a negative binomial model.

Uterine fecundity (number of *vitellogenic oocytes* plus *litter size*) ranged from 2 to 64 (mean = 28.72, SD = 15.44). There was a significant relationship between *female size* mm TL and *uterine fecundity* (Linear Regression, n=19, R^2 = 0.24, p = **0.04**). The best fit was provided with a negative binomial model.

$$Uterine\ fecundity = 1.11 + 0.32\ female\ size\ (mm\ TL) + Season + \varepsilon_i \qquad [11]$$

Pup length (when large enough to be visible with the naked eye) ranged from 20 to 357 mm (mean = 179.14, SD = 116.66). There was a significant relationship between *female size* mm TL and *pup length* (Linear Regression, n = 21, R^2 = 0.86, p < **0.05**). The best fit was provided with a linear regression.

$$Pup\ Length = 2.45 + 3.76\ Length\ of\ female\ (TL\ mm) + Season + \varepsilon_i \qquad [12]$$

The ratio of male to female embryos was 1: 0.99, and was not significantly different from a sex ratio of 1:1 (x^2 = 91.23, DF = 21, p = 0.97). An equal number of embryos were found in each uterus (paired *t*-test, DF = 14, p = 0.18). The largest embryos (382 mm) were observed in October.

The smallest embryo measured in summer was 17 mm TL. Length of pups increased towards the end of the year with a peak in spring (Figure 2.8). Full term embryos were visible in spring. By late spring (November) most *M. mustelus* caught were post-partum. In early summer, 44 % of female *M. mustelus* were pregnant. Parturition was assumed to occur between October and November, as free-swimming neonates were observed during November and December. The smallest free-swimming pup (381 mm) with an open umbilical scar was observed in December. Neonates with open or partially closed umbilical scars measured between 381 to 482 mm TL. It is therefore assumed that birth size starts at 381 mm TL.

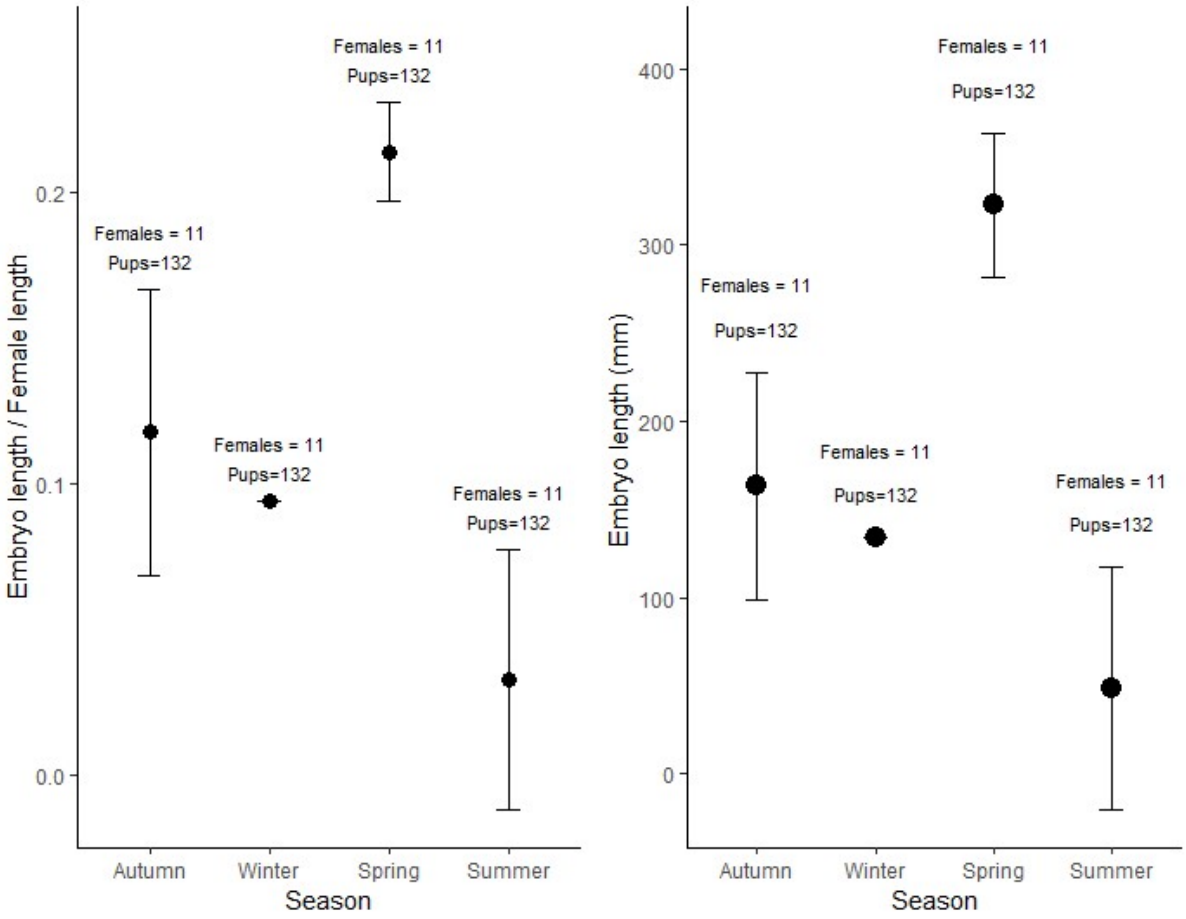


Figure 2.8. The mean ± standard error of the ratio *M. mustelus* embryo length mm TL and embryo length mm TL in relation to female length mm TL by season in the Langebaan Lagoon. The litter size and number of mothers are indicated above the error bars.

Males

Description of reproductive tract and maturity states

Visual inspection showed that the reproductive tract of male *M. mustelus* is symmetrical with two similarly sized and functional testes (Figure 2.9). Prior to the onset of maturity, the shape of the reproductive tract of male *M. mustelus* changes; the ductus deferens changes from narrow and threadlike to heavily coiled; the seminal vesicle increases in size from the posterior end while the testes increase in size and complexity. Sperm production precedes the calcification of the clasper and the ability of the claspers to fully articulate (Figure 2.10).

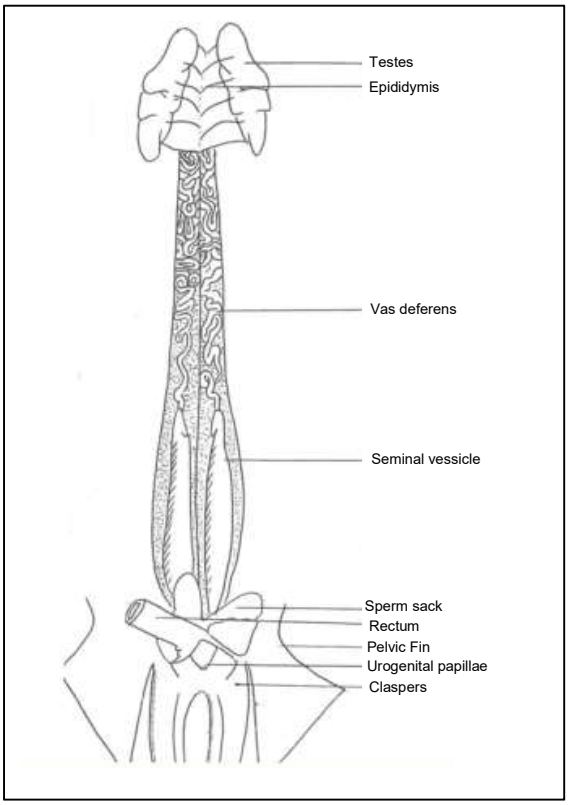


Figure 2.9. The reproductive tract of a mature male *M. mustelus.*

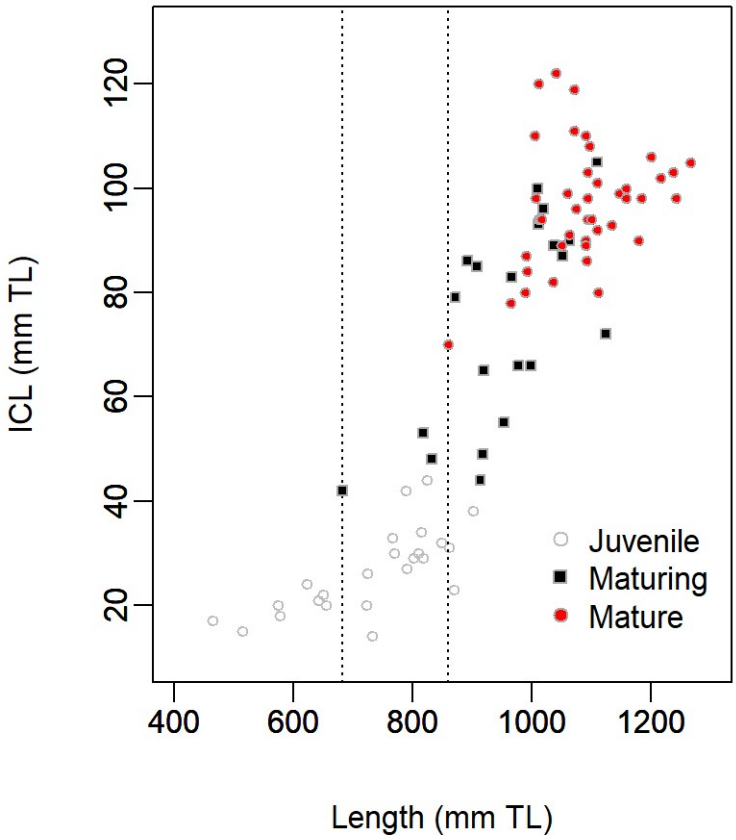


Figure 2.10. The relationship between clasper length (CL) and total length TL for *M. mustelus* from Langebaan Lagoon (juvenile, maturing and mature males). Vertical lines indicate the length where the first maturing and mature individuals were observed.

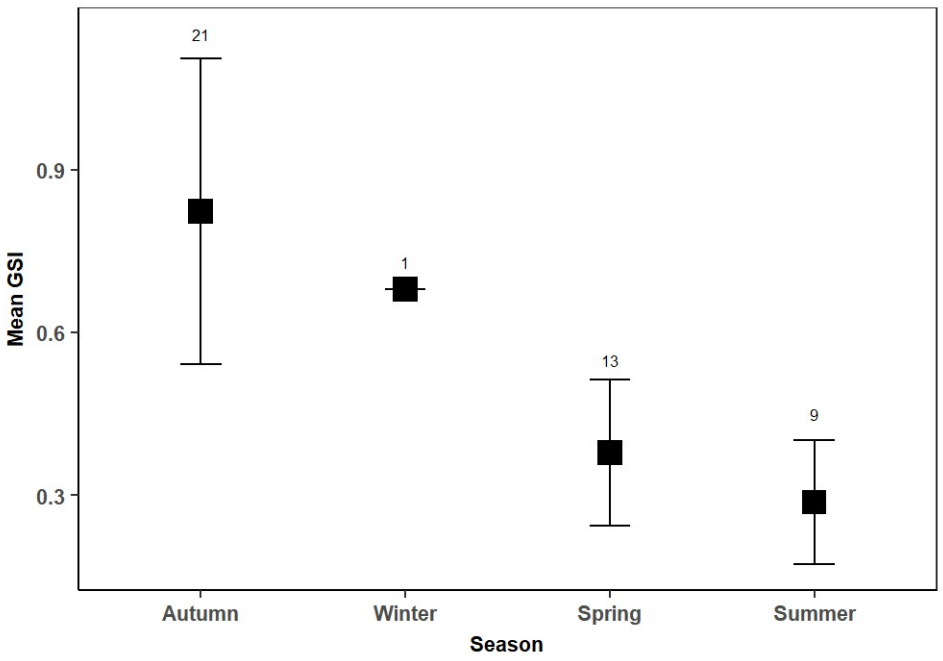


Figure 2.11. The mean ±standard error of the gonado-somatic index (GSI) by season for male *M. mustelus* in Langebaan Lagoon. Sample numbers per month are indicated above the error bars.

On average mature male GSI was 0.6 % (SD = 0.3, range 0.1-1.6 %). GSI % decreased between autumn at 0.8 % (SD = 0.3, range 0.3-1.6 %) and summer at 0.3 % (SD = 0.1, range 0.2- 0.5 %). GSI varied significantly among seasons (ANOVA, $F = 48.84$, $p < 0.05$) (Figure 2.11).

Diet of *M. mustelus*

Of the 217 stomachs examined, 189 contained prey items. *M. mustelus* diet composition indicating the percentage at which different items occur (%N) and frequency of occurrence (%F) is shown in Table 2.2. The identified prey items belonged to seven families of crustaceans, two families of chondrichthyes, and unidentified teleosts, molluscs and nematodes (Table 2.2). Crustaceans were by far the most dominant and frequent prey (92.4 %N, 96.4 %F), followed by teleosts (0.5 %N, 1.5 %F), chondrichthyes (0.5 %N, 1.0 %F) and molluscs (0.5 %N, 1.01 %F). The few sharks which preyed on teleosts were larger than 800

mm TL. Only sharks larger >1000 mm TL consumed other chondrichthyans. The ingested chondrichthyans were *Acroteriobatus blochii* and *M. mustelus*. One instance of cannibalism on a neonate shark was recorded. Sex (ANOSIM, *R* statistic = 0.002, p = 0.53), maturity (ANOSIM, *R* statistic = -0.03, p = 0.81), and size class (ANOSIM, *R* statistic = -0.08, p = 0.79) did not account for variation in prey composition found and no ontogenetic effects in prey selection were observed.

Table 2.2 *M. mustelus* diet composition indicating the percentage at which different prey items occur (% N) and the frequency of occurrence (% F).

Prey item	% N	% F
CRUSTACEANS	92.42	93.47
Hymenosomatidae		
Hymenosoma orbiculare	53.19	68.34
Nautilocoryste ocelata	0.39	2.01
Upogebiidae		
Upogebia africana	25.85	60.30
Callianassidae		
Callichirus kraussi	7.26	19.10
Portunidae		
Ovalipes trimaculatus	3.07	6.53
Varunidae		
Cyclograpsus punctatus	2.04	3.02
Unidentified crabs		
Palinuridae		
Jasus lalandii	0.37	1.01
Isopoda		
Paridotea ungulata	0.25	2.51
MOLLUSCS	0.52	1.01
Cephalopoda		
Octopodidae		
Unidentified octopus	0.50	0.50
Gastropods	0.01	0.50
TELEOSTS		

Table 2.2 continued

Unidentified teleosts	0.54	1.51
CHONDRICHTHYES	0.52	1.01
Triakidae		
Mustelus mustelus	0.50	0.50
Rhinobatidae		
Acroteriobatus blochii	0.01	0.50

Growth of *M. mustelus*

Precision Analysis

Due to the small number of vertebrae collected, the small size of some of the samples and high rate of sample loss during sectioning, only 125 vertebrae were available for age and growth analysis. Three readers each read the vertebrae independently of each other, without knowledge of the length and in a randomized order. When age estimates per vertebrae for all readers was combined the APE for each vertebra was large (mean = 10.8 %, range = 0-19.2 %, SD = 4.6 %), with only 71 vertebrae with acceptable APE scores of under 20%. The combination of reader A and C yielded a lower APE (mean = 8.7 %, range = 0-19.3 %, SD = 4.3 %), with 80 vertebrae with acceptable APE scores under 20%. The combination of reader B and C yielded a total number of 87 vertebrae with acceptable APE scores under 20% (mean = 8.7 %, range = 0-19.3 %, SD = 4.3 %). Age estimates for reader A and B yielded the highest number of vertebrae with acceptable APE scores under 20% at 91, (mean = 8.2 %, range = 0-119.6 %, SD = 4.9 %). Regression analysis showed that the best fit was provided between reader A and B. The null hypothesis that the slope of the regression = 1 failed to be rejected ($p = 0.05$) and the intercept estimate was significantly different from zero ($p > 0.05$). Therefore, age estimates from readers A and B were averaged and used as age estimates representing *M. mustelus* in Langebaan Lagoon. Age estimates ranged between 0 and 13

years, with sharks measuring between 608 mm and 1779 mm (n = 91). IAPE for readers *A* and *B* was 8.05 %. Age-length keys are provided in Tables 2.3-2.5.

Table 2.3 Age at length key for combined sex *M. mustelus* (n=95).

Total length (mm)	Age													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
300	1													
400	3													
500														
600			3		1									
700				1	1									
800				2	3	2	3							
900					2	2	1	2	2					
1000					2	8	3	4	3				1	
1100					3	2	5	4	3	1			1	
1200					1		1	4	2	1				
1300							2		2			1		
1400									3	1	1			
1500										1		1	1	1
1600										1				
1700									1				1	

Table 2.4 Age at length key for female *M. mustelus* (n = 53).

Total length (mm)	Age													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
300	1													
400	2													
500														
600			2		1									
700				1										
800				2	1	1								
900					2			1	2					
1000						3	2		1					
1100						1	3		3	1			1	
1200					1			2	2					
1300							2		2			1		
1400									3	1	1			
1500										1		1	1	1
1600										1				
1700									1				1	

Table 2.5 Age at length key for male *M. mustelus* (n = 42).

Total length (mm)	Age													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
300														
400	1													
500														
600			1											
700					1									
800					2	1	3							
900						2	1	1						
1000					2	5	1	4	2				1	
1100					3	1	2	4						
1200							1	2		1				

Growth of M. mustelus

The von Bertalanffy growth parameters are summarized in Table 2.6. The sex specific von Bertalanffy growth curves are shown in Figure 2.12. The growth parameters for the combined sexes indicate a maximum asymptotic total length (L_{∞}) of 1594.38 mm TL, with a Brody's growth coefficient (K) of 0.15 year^{-1}, and an age at zero length (t_0) of -2.01 (n = 95). Female *M. mustelus* attain a L_{∞} of 1897.73 mm TL, with a K of 0.11 year^{-1} and a t_0 of -2.08 (n = 53). Male *M. mustelus* reach an L_{∞} of 1120.13 mm TL, a K of 0.41 year^{-1} and a t_0 of -1.26 (n = 42).

Estimation of error (CV %) of growth parameters yielded large values for combined sharks ($CV_{L\infty}$ = 9.9 %, CV_K = 22.6 %, CV_{t0} = 17.8 %), females ($CV_{L\infty}$ = 8.3 %, CV_K = 22.7 %, CV_{t0} = 15.7 %) and males ($CV_{L\infty}$ = 6.2 %, CV_K = 33.0 %, CV_{t0} = 38.3 %) and for the parameter t_0. There was a significant difference for the growth between sexes (x^2 = 22.67, DF= 3, $p < 0.05$).

Table 2.6 Von Bertalanffy growth model parameters for *M. mustelus* and 95 % confidence intervals (CI). Results have been presented for combined sex data, and female- and male-specific data.

Parameter	Point estimate	95 % CI Range	CV (%)
Combined sexes (n = 95)			
L_∞ (mm TL)	1594.38	(1375.49 - 2000)	9.86
K ($year^{-1}$)	0.15	(0.10 - 0.23)	22.62
t_0 (years)	-2.01	(-2.86 - -1.40)	17.76
Females (n = 53)			
L_∞ (mm TL)	1897.73	(1524.61 - 2000)	8.28
K ($year^{-1}$)	0.11	(0.10 – 0.19)	22.73
t_0 (years)	-2.08	(-2.75 - -1.47)	15.65
Males (n = 42)			
L_∞ (mm TL)	1120.13	(1041.66 – 1301.30)	6.18
K ($year^{-1}$)	0.41	(0.21-0.77)	33.00
t_0 (years)	-1.26	(-2.67 - -0.66)	38.33

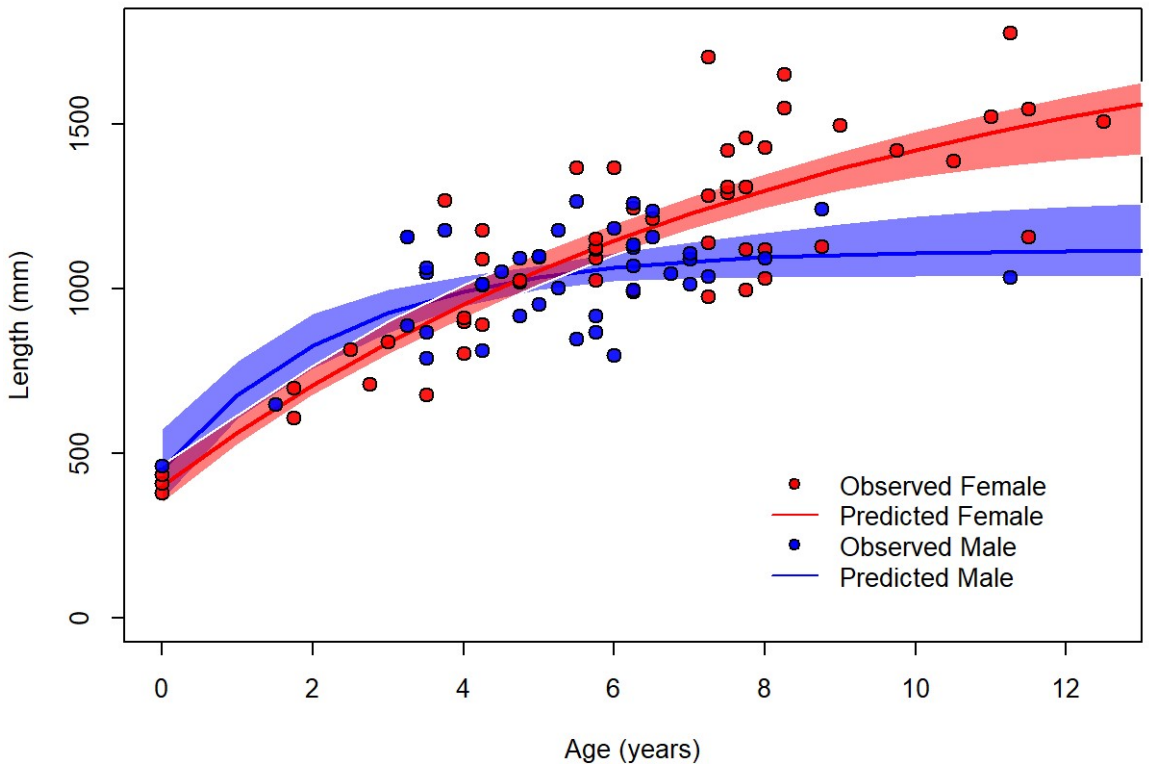


Figure 2.12 The von Bertalanffy growth curves of *M. mustelus* from Langebaan Lagoon by sex. Shaded areas show confidence intervals

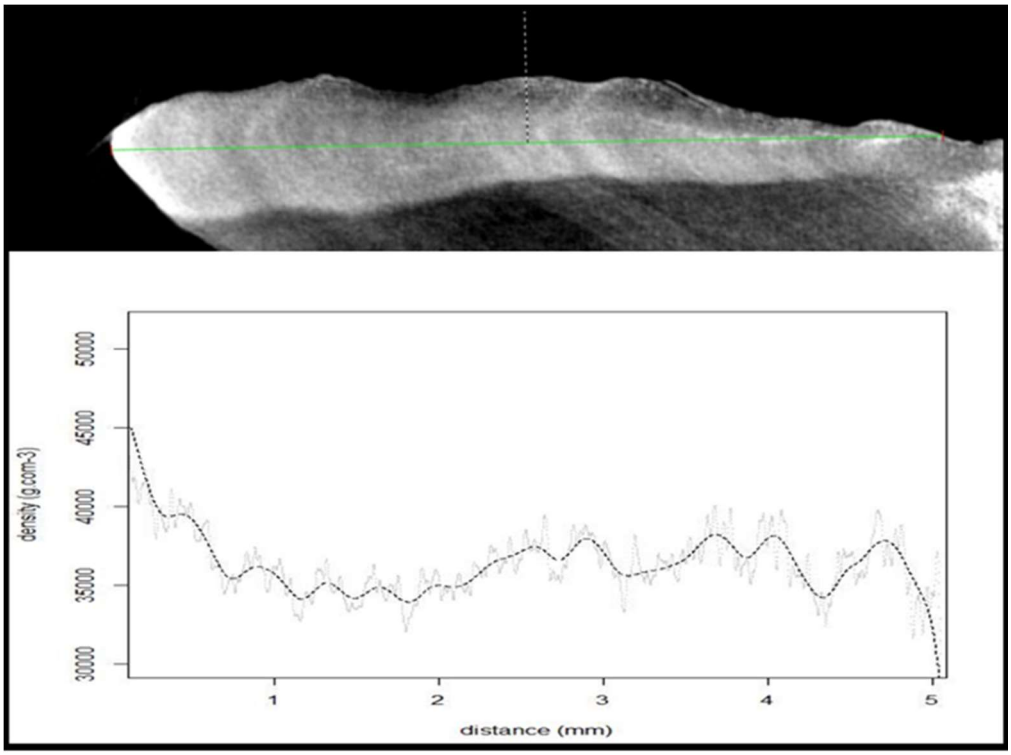
Alternative aging method: micro-CT

Age estimates from readers *A* and *B* on virtual sections (VS), density calibration plots (DCP) and virtual sections and density calibration plots combined are given in Table 2.7. Observed ages for the six randomly selected VS ranged between five and ten. Observed ages when using the Micro-CT generated DCPs ranged between three and nine. Observed ages obtained through the combined use of DCPs and VS as shown in Figures 2.13-2.15 yielded estimates between three and nine. Precision varied between different methods of reading. Precision analysis was calculated as above and used as an indication of which method provided more accurate estimates.

Table 2.7 Age estimates from readers a and b on virtual sections (VS), density calibration plots (DCP) and virtual sections and density calibration plots combined taken from *M. mustelus* vertebrae.

Sample	Length (mm)	Sex	Reader *a*			Reader *b*		
			VS	DCP	Combined	VS	DCP	Combined
14	890	f	8	4	9	10	3	6
24	699	f	5	2	3	9	3	4
42	724	m	6	5	7	8	4	5
89	1369	f	7	6	7	9	5	3
105	536	f	6	9	6	7	8	3
18	990	m	5	7	8	5	6	8

Age estimates using the DCPs where the most accurate with an IAPE of 7.6 %. All age estimates were only off by 1 count. APE scores ranged from 3.9 to 13.3 % (average = 7.6 %, SD = 3.4 %). Age estimates from VS were used as a proxy for estimates that would be obtained from reading vertebrae. These estimates were similar to those obtained through DCPs, however the IAPE was larger 8.2 %. APE scores for each vertebra ranged from 0 to 19.1 % (average = 8.2 %, SD = 6.3 %). Estimates obtained from VS tended to be larger for reader a than reader b. Age estimates from combined DCP and VS yielded a higher IAPE of 13.8 %. APE scores ranged from 0 to 26.7 % (average = 13.8 %, SD = 9.5 %). The null hypothesis that the slope of the regression equals one failed to be rejected ($p > 0.05$) for all t-tests between the primary and secondary reader and none of the intercept estimates was significantly different from zero ($p > 0.05$).



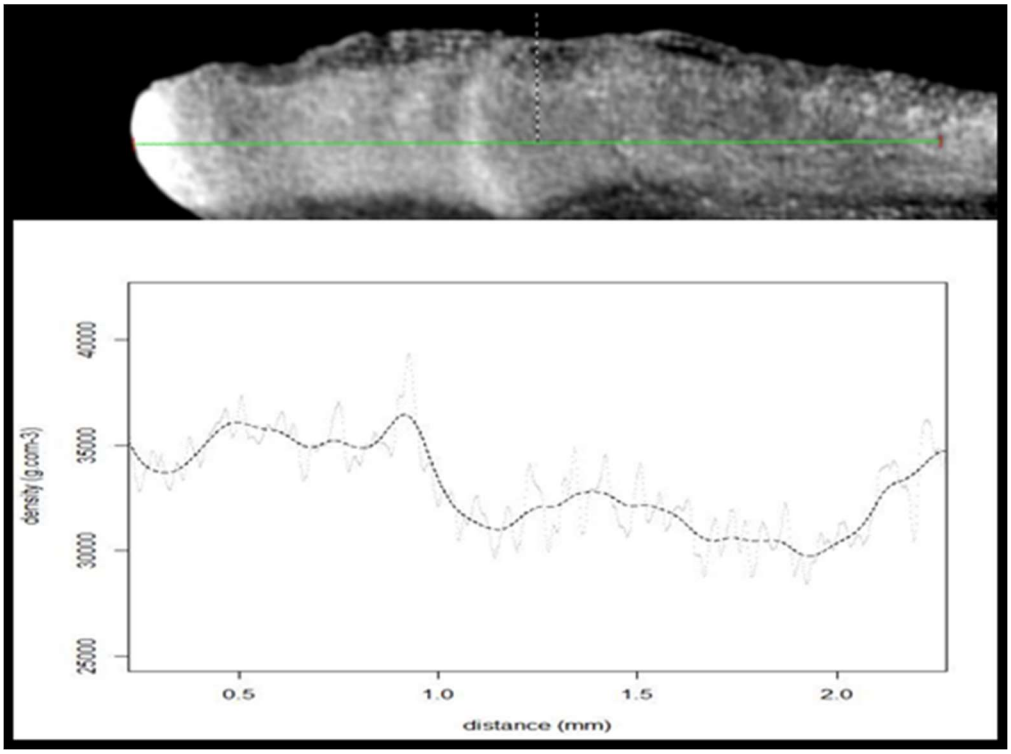
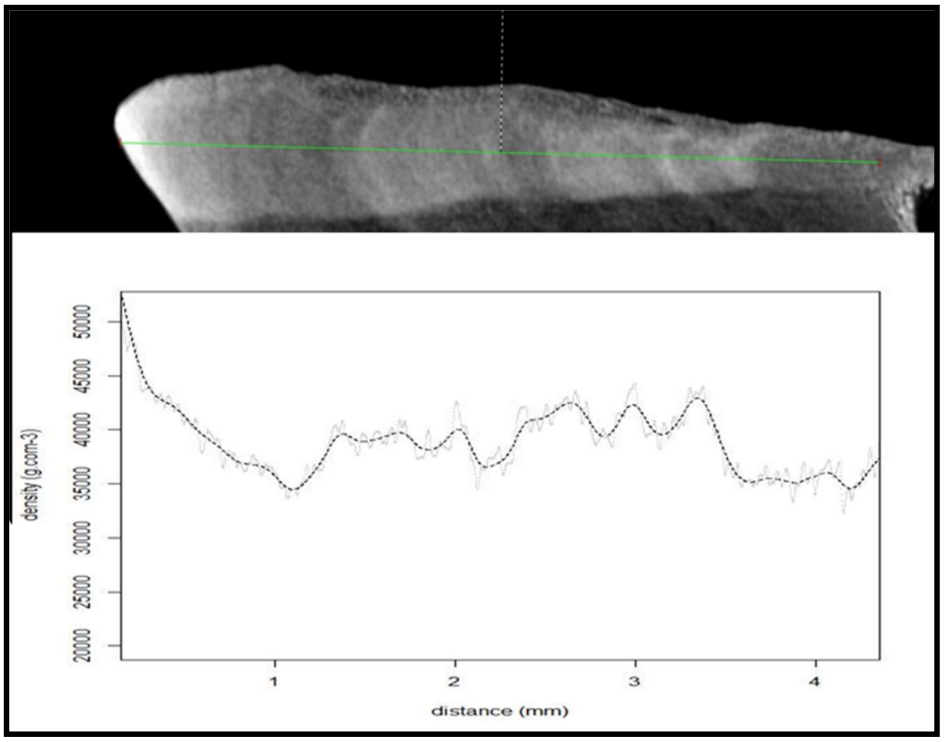


Figure 2.13. Reconstructed 3D virtual microCT sections with an overlay showing absolute density calibration (g/cm^3) across the corpus calcareum of *M. mustelus* vertebrae taken from shark numbers 14 and 24.



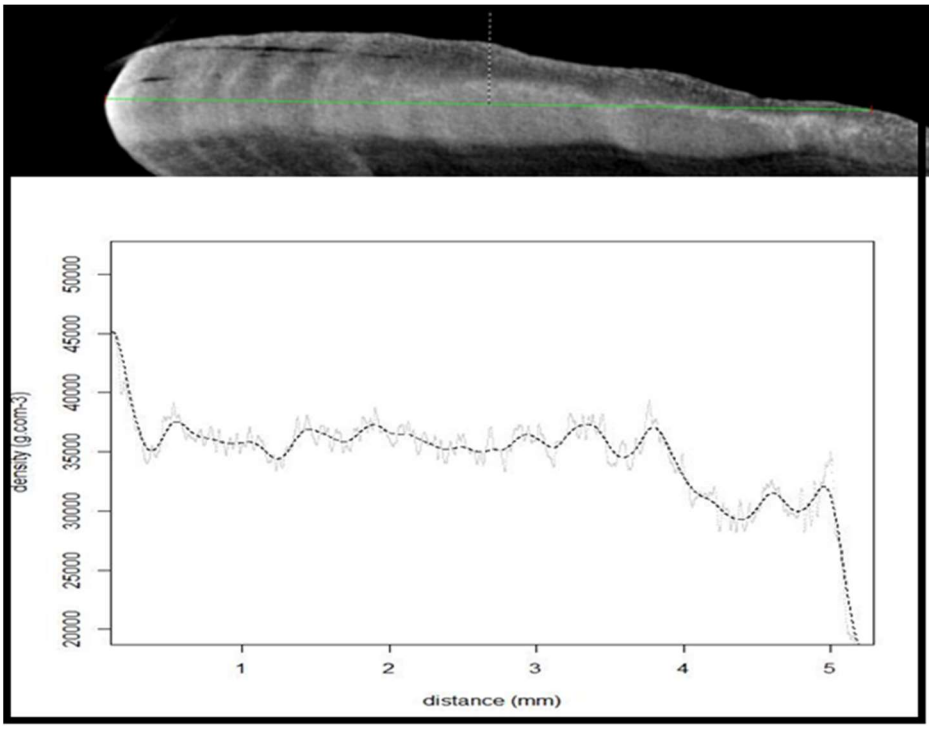


Figure 2.14. Reconstructed 3D virtual microCT sections with an overlay showing absolute density calibration in g. cm^3- across the corpus calcareum of *M. mustelus* vertebrae taken from shark numbers 42 and 89.

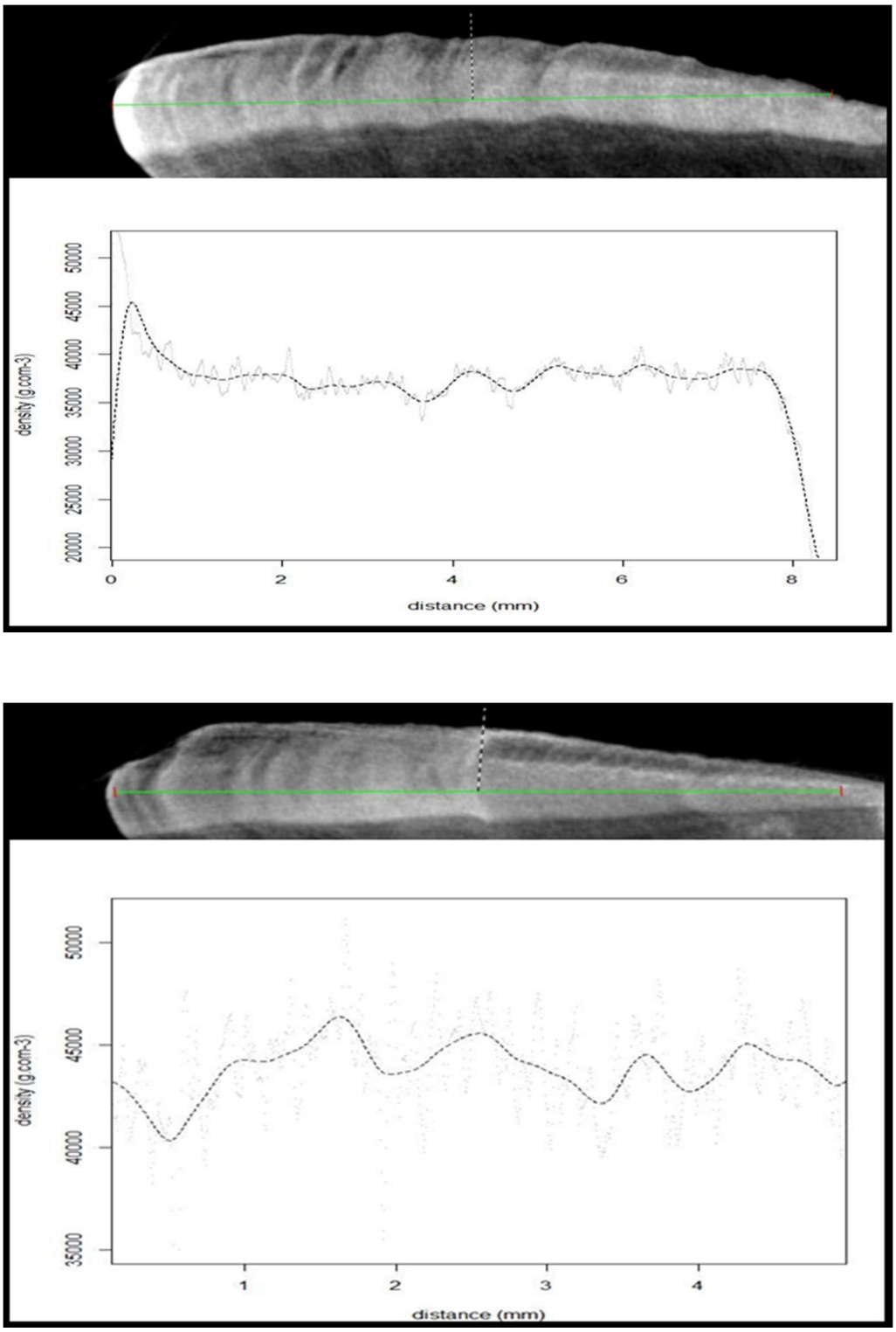


Figure 2.15. Reconstructed 3D virtual microCT sections with an overlay showing absolute density calibration in g. cm^3- across the corpus calcareum of *M. mustelus* vertebrae taken from shark numbers 105 and 118.

Maturity

In males, the relationship between the OCL and TL was best described as a sigmoidal curve with three stages: (1) between 400-800 mm TL there was low growth of OCL from 14-44 mm (SD = 8.10), (2) rapid growth was evident between 800 - 1000 mm TL with OCL increasing from 44 - 105 mm (SD = 19.80), and finally (3) slow growth between 1100 and 1300 mm of OCL from 105 to 122 mm (SD = 16.80) (Fig. 2.10). Claspers of sharks larger than 1126 mm TL were always calcified and were fully articulated, indicating the ability to copulate. The smallest mature male collected in this study was 860 mm TL, while the largest immature male was 1125 mm TL. The smallest male with claspers able to articulate was 577 mm, whereas the smallest male with sperm present was 664 mm. A transition stage for sperm production was evident in males between 800-900 mm, whereas all males larger than 1100 mm TL showed evidence of sperm inside the sperm sacs. The majority of individuals larger than 1000 mm TL had claspers that were able to rotate anteriorly.

The length at which 50 % of females were mature was estimated at 1194.8 mm TL (Table 2.8, Figure 2.16), corresponding to an age of 6.2 years. The length at which 50 % (L_{50}) of the males were mature was estimated at 967.4 mm TL (Table 2.8, Figure 2.16), corresponding to an age of 3.2 years. The length at which 50 % of *M. mustelus* combined sexes were mature was estimated at 1016.8 mm (Table 2.8, Figure 2.16), corresponding to an age of 4.5 years. The length at 50 % maturity was significantly different between sex (x^2 = 45.46, DF = 3, p < **0.05**).

Table 2.8 Length at 50 % maturity for *M. mustelus,* model parameters and 95 % confidence intervals (CI). Results have been presented for combined sex data, and male- and female-specific data.

Parameter	Point estimate	95 % CI Range	CV (%)
Combined sexes (n = 217)			
L_{50} (mm TL)	1016.75	(983.20-1058.69)	1.81
delta	64.64	(41.89-99.20)	22.81
Females (n = 123)			
L_{50} (mm TL)	1194.88	(1148.53-1243.13)	1.90
delta	64.70	(11.17-93.7)	29.49
Males (n = 94)			
L_{50} (mm TL)	967.44	(929.49-1005.84)	2.00
delta	68.13	(41.92-96.48)	22.95

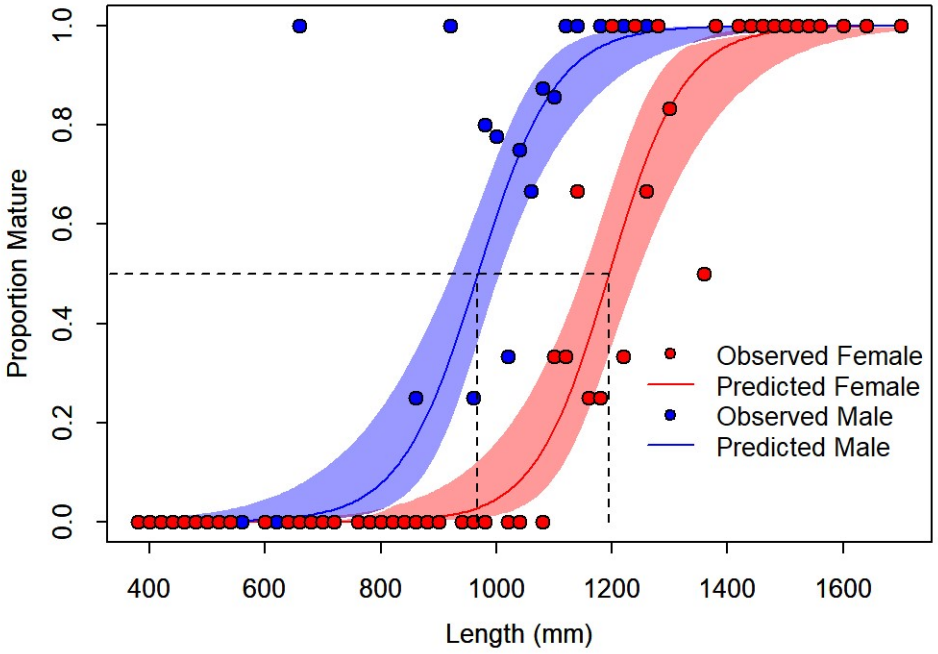


Figure 2.16. The proportion of *M. mustelus* that were mature in each 200 mm TL category and the fitted logistic curve for each sex. Shaded areas represent confidence intervals.

DISCUSSION

Body size

In Langebaan Lagoon *M. mustelus* are caught year-round, but more frequently in summer and autumn. All size classes of sharks are caught. During winter fewer samples were collected either because sharks were scarce inside the Langebaan Lagoon or they reduce their feeding rates during the colder winter months. The largest female sampled in this study was 1734 mm TL, which approximates the previous maximum recorded length in South Africa of 1732 mm (Smale and Compagno, 1997). The largest male in this study was 1267 mm TL, which is smaller than the largest male recorded in South Africa, namely 1450 mm TL. Tagging expeditions in Langebaan Lagoon (da Silva, unpublished data) sampled sharks larger than the reported maximum sizes at 1765 mm TL for females and 1579 mm TL for males. In addition, during angling surveys conducted by UCT a large male of 1515 mm TL was caught.

M. mustelus in the Saldanha embayment hosts the largest females and males recorded from six regions (Table 2.9). Previously, the largest female shark measured in Langebaan Lagoon was 115 mm larger than that recorded anywhere else, and the largest male was 312 mm larger than the largest measured males (from tagging study). Individuals of two species of teleost fish in the lagoon grow faster and attain greater maximum lengths then conspecifics in more eastward locations. *Spondyliosoma emarginatum* in Langebaan Lagoon are larger than in other areas in South Africa and have a faster growth rate (Tunley *et al*., 2009). A similar increase in growth rate and size inside the lagoon has also been shown for *Rhabdosargus globiceps* (Griffiths, 2000). The Saldanha embayment is nutrient rich due to frequent wind-induced upwelling on the West Coast (Tunley *et al.*, 2009). The high productivity within the embayment supports large beds of *Gracilaria verrucosa* and *Zostera capansis* which in turn supports high densities of prey items for these fish and *M. mustelus* (Tunley *et al.*, 2009).

This chapter highlighted the direct impact of the Langebaan Lagoon Marine Protected area as large sharks are protected from fishing activities.

Females are larger than males, in South Africa and elsewhere (Saïdi *et al.*, 2008; Goosen and Smale 1997) (Table 2.9). The difference among the sexes is substantial with an average 220 mm difference between females and males (range 60 – 437 mm, SD = 135 mm). Similar to *M. mustelus*, other viviparous sharks (~ 70 % of all sharks) generally have larger females than males (Wourms and Demski, 1993). On the other hand, oviparous sharks generally have larger males than females (Wourms and Demski, 1993). Viviparous reproductive strategies with lengthy gestation periods have significant effects on female body size. These females tend to be between 10 and 16 % longer than males of the same species (Wourms and Demski, 1993; Sims, 2005). This suggests that the evolution of larger female body size in sharks arises from a viviparous reproductive mode and the resulting impact on female body size on fecundity (Sims, 2005). This was evident from this study also, and although litter size did not increase with female size, uterine fecundity and pup size did. Female habitat choice is primarily driven by a necessity to maximize offspring survival and lower predation risk over choosing optimal foraging conditions and therefore resources are important due to larger investment in reproduction (Wearmouth and Sims, 2008). Males on the other hand choose habitat based on resource availability to maximize body condition in preparation for mating activity, once this size is reached they seek out females (Wearmouth and Sims, 2008). Since larger sharks have higher absolute energy requirements than smaller sharks, males allocate energy towards growth up to a certain size when body condition is optimal for reproduction (Sims, 2005). This study shows that adult females occur in the same area as the pups.

Pigmentation

A large degree of pigmentation in the form of black spots was observed in sharks larger than 1000 mm TL. Patterning of more than 15 % of the body was related to shark size. The origin of southern African *Mustelus* species, at least those within the placental non-white spotted clade such as *Mustelus mustelus* and *M. mosis* are as a result of two to perhaps three (in the case of *M. mosis*) separate colonisation events from the Mediterranean (Maduna, 2017). A number of studies have reported pigmentation in some populations of *M. mustelus* (da Silva, 2007; Maduna, 2017; Marino *et al*., 2014) with some individuals resembling *Triakis megalopterus*,complicating species identification (da Silva *et al.*, 2015). Pigmentation in the form of black spots are never found in *M. mustelus* from the Mediterranean (Marino *et al.*, 2014; Cariani *et al.*, 2017). However, similar patterning positively correlated to individual size has been documented for *M. punctulatus* (Marino *et al.*, 2014; Cariani *et al.*, 2017). It is likely given similar patterning in other *Mustelus* from the placental clade that this pigmentation is generic. In addition, given the lack of patterning in Mediterranean individuals it is possible that patterning may indicate species divergence and should be investigated in future. Also, since pigmentation only occurs in older maturing or mature individuals it is likely that the gene involved in spotting is related to the maturation process.

Reproductive biology

Ovulation in *M. mustelus* in Langebaan Lagoon occurred in spring from November to December, similar to other locations in South Africa (Smale and Compagno1997). Although mating behaviour was not observed in this study, the male GSI trend suggests that this occurs in the first half of the year. The exact period is difficult to determine due to the low sample size of mature males over winter (n=1), however this coincides with what was found previously in South Africa (Smale and Compagno 1997). As expected, mating in northern

hemisphere *M. mustelus* occurs between April and June in Senegal (Capapé *et al*., 2006), January and May in Mauritania (Khallahi, 2004), May in the Gulf of Tunis (Capapé, 1974) and May to June in the Gulf of Gabés (Saïdi *et al*., 2008). The presence of fully developed embryos in September and observations of the smallest free-swimming neonates with umbilical scars suggests that parturition occurred in October and November. As expected, parturition in northern hemisphere *M. mustelus* occurs in spring and summer between April and July in Senegal (Capapé *et al*., 2006), February and June in Mauritania (Khallahi, 2004), April and May in the Gulf of Tunis (Capapé, 1974) and June and July in the Gulf of Gabes (Saïdi *et al.*, 2008). Short periods between parturition and ovulation is common for mustelids (Francis and Mace, 1980), although the common trend is for parturition, mating (or males ready to mate) and ovulation to occur within 3 months (Capapé, 1974, Capapé *et al*., 2006 and Saïdi *et al*., 2008).

Female reproductive trends in ovarian weight, GSI, embryo length and development suggest a gestation period of 11 months. A peak in GSI prior to ovulation is common, with mating usually occurring during the brief period from the end of parturition to the beginning of the next ovulation (Teshima, 1974; Conrath *et al.*, 2002; *inter alia* Saïdi *et al*., 2008). During pregnancy, the passage of spermatozoa is obstructed by embryos and intrauterine compartments (Saïdi *et al*., 2008). This study and that of Smale and Compagno (1997) could not conclusively confirm whether reproductive periodicity was annual. However annual reproductive periodicity is common for the genus *Mustelus* with lengthy periods of sperm storage of up to a year (Conrath and Musick, 2002).

Fecundity in elasmobranchs is often determined by counting the number of oocytes and embryos within the uterus (Conrath, 2005). This may be problematic as reproductive failure

may occur during gestation with a number of pups not surviving the gestation phase (White *et al.*, 2001). Often during the stress of capture, elasmobranchs have been shown to abort pups especially if close to parturition (Conrath, 2005). This can be overcome by counting the number of parturition scars in addition to the pups in the uterus. In this study, however, as all aborted pups following capture were kept separate and therefore, counting scars was not necessary. Irrespective, this study potentially overestimates litter size as it was determined during all stages of gestation. Therefore, estimates of uterine fecundity are considered at their upper limit. Similar issues arise when using oocyte count as an estimate of ovarian fecundity (Wetherbee, 1996). Although some studies have found uterine and ovarian fecundity to be similar (Capapé *et al.*,1990; Peres and Vooren, 1991; Wilson and Seki, 1994), others found that ovarian fecundity is notably higher than number of pups, indicating absorption of oocytes. Larger females had increased uterine fecundity. However, larger females did not have larger litters as previously found by Smale and Compagno (1997). Pups from larger mothers were significantly larger than those from smaller females. An increase in fertility with size of female is a common phenomenon and has been shown in many species of sharks (Nakano, 1994; Conrath, 2005).

Maturing males are seen as small as 682 mm TL with an increase in clasper length; however, calcification was only seen as early as 818 mm TL. Trends in male GSI suggest that spermatogenesis starts in December. Spermatozoa accumulate in the seminal vesicle until June. Males with swollen seminal vessels containing large amounts of sperm were observed in this study in the month of May in one shark, however all males over 800 mm TL had sperm present in sperm sacks to some degree. Male GSI trend suggests that sperm accumulates the first half of the year, although this trend is obscured with low sample numbers in winter. This does not match the female cycle, with a delay of approximately six

months between peak sperm production and ovulation. Therefore, either mating occurs in the first half of the year with females storing sperm until ovulation or sperm is stored by males or a combination of both.

In this study, the delay in peak male fertility (i.e. sperm production) and ovulation given the questions around mating period could indicate storage of sperm of up to six months. Sperm storage by females in oviducal glands has been observed in *M. mustelus* from Langebaan Lagoon (Maduna *et al*., 2017). The ability of females to store sperm in the oviducal glands has been documented in several species including *C. obscurus*, *Rhizoprionodon terraenovae*, *Prionace glauca* and *Sphyrna tiburo* (Pratt, 1993). Storage time varies between species, *R. terraenovae* store sperm for short periods generally with delayed insemination (Pratt, 1993), alternatively nomadic species such as *P. glauca* can store sperm for a period of months to years (Pratt, 1993). Additionally, some groups of sharks have been shown to exhibit male sperm storage such as *Carcharhinidae, Scyliorhinidae, Sphynidae* and *Rajidae* (Pratt and Tanaka, 1994). Sexual dimorphism with larger females is common in elasmobranchs and associated with polyandry and multiple paternity (Wourms and Demski, 1993). Polyandry, in which one female reproduces with multiple males has been described in *M. mustelus* from Langebaan Lagoon (Maduna *et al.*, 2018) as well as *M. henlei* (Byrne and Avise, 2012), *Ginglymostoma cirratum* (Saville *et al*., 2002), *Scyliorhinus canicula* (Griffiths *et al*., 2011) and *C. plumbeus* (Daly-Engel *et al*., 2007).

Langebaan Lagoon as a nursery ground

The presence of juveniles, neonates as well as pregnant females within the lagoon indicates that it may be a nursery ground. Sharks were collected inside the closed area as they are infrequently caught outside (da Silva, unpublished catch data, Department of Agriculture,

Forestry and Fisheries, unpublished data, University of Cape Town, unpublished data). From data collected through standardized angling with equal angling effort inside and outside the LMPA only eight *M. mustelus* were caught outside the LMPA between 2004 and 2015. Similarly, neonates and juveniles are uncommon outside the closed area (University of Cape Town, unpublished data). Although length frequency data was not compared due to the difficulty in catching sharks outside the LMPA, it is clear from sampling in this study that large concentrations of neonate, juvenile and mature sharks are only found within the closed area and on occasion around the closed area boundary. According to the definition provided by Heupel *et al.,* (2007), a nursery ground has the following attributes: 1) newborn or young-of-the-year sharks are more commonly found within a nursery area than outside, 2) newborn or young-of-the-year sharks have a tendency to remain inside the area for extended periods within the area and when they leave they often return and 3) that the area or habitat is repeatedly used across years by newborn or young-of-the-year. The general absence of small sharks outside the closed area suggests that they are more common inside the LMPA than outside and that they remain inside the area for extended periods, thereby providing confirmation of Criteria 1 and 2. The remaining Criteria 3 will be evaluated in Chapter 3.

Diet of *M. mustelus*

Crustaceans formed the largest part of the diet of *M. mustelus* in Langebaan Lagoon. Three species of crustaceans; *Hymenosoma orbiculare*, *Upogebia africana* and *Callichirus kraussi* (Stebbing, 1900) were commonly found in the stomachs. Other studies found that crustaceans occurred in 50 %, 70 % and 59 % of *M. mustelus* sampled in the rest of South Africa (Smale and Goosen, 1997), Gulf of Gabes (Saïdi *et al*., 2008) and Gulf of Tunis (Capapé, 1974), respectively. Other studies showed a large variety of prey consumed including teleosts and molluscs. In the lagoon, these prey items made up less than 8 % of prey items. *C. kraussi* and

U. africana are dominant members of the macrobenthos in Langebaan Lagoon (Day, 1959; Puttick, 1977; Nel and Branch, 2013). These prawns occupied distinctly different habitats. High densities of *U. africana* are found within the *Zostera* beds on the eastern and southern shores with fine sediment (Nel and Branch, 2013). Low densities were recorded on the upper and lower sandbanks at most sites but was absent from the sub-tidal flats and deeper channels in the Langebaan Lagoon closed area (Nel and Branch, 2013). *U. kraussi* lives in permanently constructed u-shaped borrows (Nel and Branch, 2013), and it is unclear how *M. mustelus* are able to catch large amounts of burrowing crabs. Buccal pumping has been shown in Mustelids and may aid *M. mustelus* to prey on these animals (Wilga *et al.*, 2007). *C. kraussi* has a wider distribution, occurring everywhere in the lagoon except in some areas inside Saldanha Bay. The highest abundance of *C. kraussi* was found in the shallow subtidal zones where water movements are more pronounced and declined in deep channels. *C. kraussi* and *U. africana* mud prawns are seldom found in the same areas. *H. obiculare* occur within the zostera beds inside the lagoon (Day, 1959; Puttick, 1977). As a surface dwelling crustacean, it would be easy to locate despite cryptic camouflage. These habitat differences between main prey suggest that *M. mustelus* move between different areas to feed, from the submerged *zostera* beds to the shallow subtidal zones. Unusually, chondrichthyes were found within the stomachs of two *M. mustelus*. This has not been described in mustelids and may be a driver for segregation by size. In other areas in South Africa, *M. mustelus* sexually segregate with large females being found on shallower inside sandy bays (Smale and Compagno, 1997). Although limited numbers of teleosts and sharks were consumed by *M. mustelus* in this study, the trend was not strong or consistent enough to be significantly different and therefore no ontogenetic change in diet was found for *M. mustelus* in the lagoon. The tendency for sharks to shift diet to a wider range of prey including cephalopods and teleosts with age has been shown by both Saïdi *et al*., (2009) and Smale and Compagno

(1997). The stability in diet may be related to the large numbers of crustaceans present inside the lagoon (Nel and Branch, 2013).

Growth of *M. mustelus*

Modelled length at age revealed that *M. mustelus* grow rapidly, reaching an asymptotic length of 1594 mm TL, and a maximum observed age of 13 for combined sexes. Modelled maximum length at age for females was 1898 mm TL, with males at a lower 1120 mm TL. Previous studies completed by Goosen and Smale (1997) which included samples from Langebaan Lagoon estimated larger asymptotic lengths of 1989 mm TL, 2049 mm TL, and 1451 mm TL for combined sexes, females and males, respectively. Similarly, da Silva (2007) estimated these as 1946 mm TL, 2202mm TL and 1713 mm TL, for combined sexes, females and males excluding samples from Langebaan Lagoon, respectively. Maximum observed ages from previous studies were estimated at 24 (Goosen and Smale 1997) and 25 (da Silva, 2007), respectively. Maximum age at 13 estimated in this study was half of what was previously estimated for this species (Goosen and Smale, 1997; da Silva, 2007) in South Africa. The large difference in age estimates between this study and others could be attributed to the occurrence of "false" vertebral bands observed in this study. Additionally, validation of age estimates is required to determine which area within the vertebral column yields the most accurate age estimates which reflect the actual age (Officer *et al*., 1996). Estimates taken from *M. antarcticus* cervical vertebrae were often lower than those from thoracic vertebrae. Since five vertebrae were originally taken from sharks, it is possible that some cervical vertebrae were included in the readings. However, initial readings prior to the discovery of the "false" vertebral brands yielded similar estimates to those of Goosen and Smale (1997).

A recent literature review by Harry (2018) indicated that ageing sharks and rays by counting growth zones on calcified structures can underestimate true age. Age was likely underestimated in nine of 29 genera and that underestimation was likely a systemic issue associated with the current methods and structures used for ageing (Harry, 2018). Vertebral growth bands cannot accurately reflect ages across life stages for New Zealand *Lamna nasus* (Nelson and Johnson, 2014), *Carcharhinus plumbeus* (Andrews *et al*., 2011), *Galeorhinus galeus* and *Carcharhinus melanopterus* (Chin *et al*., 2013). For *L. nasus*, vertebral band composition becomes increasingly narrow with increasing age or that vertebrae stopped growing (Nelson and Johnson, 2014). Similarly, for *Carcharias taurus*, Passerotti *et al.*, (2014) using bomb radiocarbon dating found maximum ages more than double that of previous studies. Vertebral growth bands have also been aperiodic such as the *Squatina californica* (Natanson *et al.*, 2002), or follow somatic growth as opposed to temporal cues such several species of wobbegong sharks (Chidlow *et al.,*2007; Huveneers *et al.*, 2013). The existence of "false" check marks, narrow vertebral band composition with increasing age and aperiodic vertebral band deposition results in problems with estimation of age, highlights the need for age validation (Passerotti *et al*., 2014).

Maximum age in this study is similar to what has been found within the genus *Mustelus*: *Mustelus antarcticus* 16+ years (Moulton *et al.*, 1992), *M. manazo* 9+ (Tanaka and Mizue, 1979) and *M. californicus* 9+ years (Yudin and Cailliet, 1990). The possibility of overestimation of maximum age was also indicated through the use of micro-computed tomography. Estimates taken from DCP were half than those taken from VS or and less than DCP and VS combined. Since DCP measures the density across the section the occurrence of an opaque growth band should coincide with a peak in density. Therefore, the use of micro-computed tomography highlighted the existence of "false" bands which may overinflate age

estimates. Since, micro-computed tomography is too costly, it is not feasible to use as an aging method for large number of samples. These new estimates of age and growth have indicated problems with previous studies, and highlighted the need to reanalyse the age and growth for *Mustelus mustelus* for other regions. Both the age and growth of *Mustelus mustelus* for South Africa and Langebaan Lagoon needs to be reanalysed and compared using micro-computed tomography, reading method by Goosen and Smale (1997) and this new reading methods. Furthermore, it is vital that age and growth estimates for *Mustelus mustelus* from South Africa and those in Langebaan Lagoon be validated using bomb carbon dating if samples are available or chemical marking. Under- or overestimation of age will have important consequences for the management of the fisheries managing this species. Lower maximum age for *M. mustelus* than previous estimated in South Africa could explain the high abundance and resilience of this species to over 20 years of industrial fishing methods (da Silva, 2007; da Silva *et al*., 2015), alternately higher maximum age increases productivity, since it increases the period that fish are reproductively active. Although underestimation in age estimates is common in Carcharhinids and Lamnids (Harry, 2018), in this case, the existence of "false" vertebral bands, low maximum age of other *Mustelus* species (< 20) and results of micro-computed tomography it was concluded in this study that age estimates of previous age estimates were overestimated.

Previous studies have shown that late maturing, slow growing species are much more susceptible to declines when exploited (Jennings *et al*., 1999; Cortés, 2002). These new estimates of age, once validated make *M. mustelus* less vulnerable to fishing pressure. This was demonstrated by Stevens (1999b) for two sharks harvested in an Australian shark fishery, *Mustelus antarcticus* with a higher overall productivity and faster growth rates provided a sustainable fishery while the *Galeorhinus galeus* with lower productivity and slower growth

rates declined in catches (Stevens, 1999b). This mirrors the trend in South Africa where previous stock assessments showed that *M. mustelus* were optimally to marginally overexploited (da Silva, 2007), while *G. galeus* had declined (Kroese and Sauer, 1998; McCord, 2005; da Silva *et al.*, 2015). A significant difference in growth between females and males was evident. Differential growth patterns are common among Carcharhinidae, including *Carcharhinus. tilstoni*, *C. sorrah* (Davenport and Stevens, 1988), *C. limbatus* (Killam and Parsons, 1989), *G. galeus* (Padovani-Ferreira and Vooren, 1991; McCord, 2005) and *M. mustelus* (Goosen and Smale, 1997; da Silva, 2007).

Females reach a larger asymptotic length (1817mm TL) than males (1113 mm TL). Males attain their asymptotic length faster than females. This has been found for other *Mustelus* species as well, e.g. *M. antarcticus* (Moulton *et al.*, 1992) *M. manazo* (Yamaguchi, *et al.,* 1996, 2000) and *M. californicus* (Yudin and Cailliet, 1990). Bimaturism (differing sizes of maturity between males and females) has been attributed to the partitioning of energy for growth in females rather than reproduction, with a delayed onset of sexual maturity (Cortés, 2000). It is beneficial for females to reach a larger size to carry pups, on the other hand males stop growing after they reach a size of "diminishing returns" (Stearns, 1967).

L_{50} was estimated at 1194 mm TL and 967 mm TL, corresponding to an age of 6.2 and 3.1 years for females and males, respectively. These new estimates are closer to what has been found for other *Mustelus* species (Francis and Mace, 1980; Francis and Maolagáin, 2000), when compared to the previous estimates by Goosen and Smale (1997) and da Silva (2007). There was a difference in length and age at 50 % maturity between females and males. The previous estimates of growth and maturity may have been overestimated. However,

validation of age and growth is crucial to confirm estimates of age and growth for *M. mustelus*.

Reproductive parameters such as litter sizes, size at maturity and maximum size increase with increasing latitudes (Stearns, 1967, 1992). Latitudinal gradients are a product of phenotypic plasticity resulting from environmental factors affecting growth such as temperature (Parsons, 1993; Yamaguchi *et al.*, 2000; Saïdi *et al.*, 2009) and food availability (Parsons 1993). The gradients in reproductive variables cannot be readily explained by latitude. *M. mustelus* in Senegal have higher maximum length, size at maturity and size at birth than those at Mauritania. However, *M. mustelus* at the Gulf of Tunis, Gulf of Gabés and the earlier South African study confirm to this trend of increasing reproductive parameters with increasing latitude. *M. mustelus* studied by Smale and Compagno (1997) included sharks from various areas within South Africa including Langebaan Lagoon. Since Goosen and Smale (1997) included samples from areas with high fishing pressure for *M. mustelus*, it is possible that differences in maximum length, TL at maturity and TL at birth are related to fishing pressure. *M. mustelus* of Langebaan Lagoon spend the majority of their lives inside the Bay (Chapter 3) where they are minimally affected by fishing, especially the large individuals targeted by the shark fishery. The commercial shark fishery in the south-western and south-eastern Cape Coasts intensively fishes inshore (da Silva 2007) and may have removed larger sharks that aggregate inshore (Smale and Compagno, 1997). Their lower maximum lengths, size maturity and litter size may also be explained by depth. Large *M. mustelus* generally aggregate in shallow warm bays (da Silva and McCord, 2013, Smale and Compagno, 1997). It is also possible that the differences in productive variables between Senegal and Mauritania are explained by fishing pressure, however due to the low level of species-specific reporting this is difficult to quantify. Environmental conditions are also not

always suitable for pupping in temperate latitudes and a prolonged gestation period increases benefit to the young by ensuring that pups are born during optimal periods (Stearns, 1992). Therefore, gestation period of *M.* mustelus from South Africa (11 months) (Smale and Compagno, 1997, current study), Gulf of Gabés (10-11 months) (Saïdi *et al*., 2008), Gulf of Tunis (12 months) (Capapé 1974) and Senegal (12 months) (Capapé *et al*., 2006) are longer than those from Mauritania (7-10 months) (Khallahi, 2004). Delayed onset of maturity is advantageous as all effort is put towards growth prior to reproduction, therefore, length at 50 % maturity is lower in Mauritania (590 – 820 mm TL males, 570-930 mm TL females) than other regions (Khallahi, 2004).

Recent genetic studies on *M. mustelus* in South Africa suggest a strong interoceanic population structure with two genetically different populations meeting at Cape Agulhas with a limited gene flow from East to West (Maduna *et al*., 2016). The work presented here corroborated this finding and indicated that *M. mustelus* from Saldanha Bay are phenotypically distinct to those from the Eastern Cape Coast. Local differences in pigmentation, growth, fecundity and diet were evident.

Sharks sampled in the study area were therefore phenotypically distinct from those from four other studied regions and represented *M. mustelus* of the southern Atlantic stock (Maduna *et al*., 2016). These represented the animals with the largest birth and maximum lengths as well as those with the largest litters. Furthermore, sharks from the area were distinct in their diet and pigmentation. This study provided some evidence that sharks are more commonly found within the closed area than outside. In addition the presence of neonates, juveniles and ovulating, pregnant and post-partum females inside the LMPA was confirmed. Thus, meeting several of the nursery ground criteria as defined by Heupel *et al.*, (2007).

Table 2.9 Summary of published *M. mustelus* reproductive parameters

	Capapé *et al*., (2006)	Khallahi (2004)	Capapé (1974)	Saïdi *et al*., (2008)	Smale and Compagno (1997)	Current study
Regions	Senegal	Mauritania	Gulf of Tunis	Gulf of Gabes	South Africa	South Africa: Langebaan Lagoon
Maximum TL(mm)	1450 (F), 1390 (M)	1100 (F), 900 (M)	1420 (F) -	1650 (F), 1445 (M)	1650 (F) 1450 (M)	1734 (F) 1515 (M)
TL (mm) at maturity (L_{50})		720 (F) 670 (M)	960 (M)	1075-1230 (F) 880-1120 (M)	1250-1400 (F) 950-1100 (M)	1194 (F) 967 (M)
TL (mm) maturity range	900-1040 (F) 820-950 (M)	590-930 (F) 570-820 (M)	1080-1170 (F)			
TL (mm) at birth	360-450 (403)	240-320	390	340-420	368-410	381-482
Litter size	4-21	1-13	12-22	4-18	2-23	2-25
Gestation period (months)	12	7-10	12	10-11	9-11	11

CHAPTER 3: QUANTIFYING THE DEGREE OF PROTECTION AFFORDED BY A MARINE RESERVE CLOSED TO FISHING ON AN EXPLOITED SHARK SPECIES

ABSTRACT

Sharks can benefit from the protection of marine protected areas (MPAs) with areas closed to fishing. However, there is little information on the degree of protection offered by closed areas to shark populations in specific scenarios. The movements of individual *Mustelus mustelus* in and adjacent to a small closed area (34 km^2) situated on the West Coast of South Africa were investigated over two years using acoustic telemetry. Sharks spent the majority of the time (in hours, average 79 %) inside the closed area and some sharks (n = 2 of 15 recorded during a full year) did not leave the reserve during the observation period. Time spent inside the closed area and the number of crossings of its boundary were strongly influenced by season. Sharks concentrated inside the closed area during summer, while they were widely distributed throughout the study area during winter months. Six sharks left the Saldanha Bay embayment during spring and winter periods for durations ranging from two to 156 days (median = 111 days). All returned to the bay within the study period. Individuals recorded over two years showed consistency in behavioural patterns and protection by the closed area, and spent an average of 74 % and 80 % of their time inside the closed area during the two study years, respectively. The extended residency of *Mustelus mustelus* within the closed area suggests that no-take area protection may be a viable management option.

INTRODUCTION

Efforts to manage the exploitation of chondrichthyans worldwide are largely inadequate (Walker, 1998; Stevens *et al*., 2000; Ferretti *et al*., 2010; Simpfendorfer *et al*., 2011; Davidson *et al.*, 2016; Dulvy *et al.*, 2017), with some exceptions (Simpfendorfer and Dulvy, 2017). Few chondrichthyan species are comprehensively assessed largely due to the fact that more than 50 % of the estimated global catch are caught as by-catch (Stevens *et al*., 2000). In the absence of other effective regulations, closed areas have been advocated as an effective conservation method to sustain some teleost and elasmobranch fisheries (Denny *et al.*, 2004; Garla *et al.*, 2006; Worm *et al.*, 2009). Fishery benefits from area closures are thought to be derived from increased abundance inside the closed area and resultant spill-over of adults and juveniles into the fished area (Gell and Roberts, 2003; Gaylord *et al*., 2005; Pelc *et al.*, 2009). The effectiveness of a closed area depends to a large degree on the spatial behaviour of species it is intended to protect (Botsford *et al.*, 2003). Until recently, migratory and widely ranging species of fish and sharks were not expected to derive much benefit from area closures (Stefansson and Rosenberg, 2006). Nevertheless, there are exceptions where closed areas are strategically placed to protect crucial life-history stages such as reproduction and nursery areas (Gell and Roberts, 2003; Kerwath *et al.*, 2009). Recent studies for several species of shark using demographic models have highlighted the importance of survival of juveniles nearing maturity to overall population growth (Gallucci *et al*., 2006; Cortés, 1999; Simpfendorfer, 1999). Therefore, the conservation of these species would increase if these juveniles occur within areas closed to fishing.

The study of the effectiveness of closed areas for fisheries management typically entails the quantification of the dispersal of eggs and the movement behaviour of adults (Tilney *et al*., 1996; Brouwer *et al.*, 2003; Gell and Roberts, 2003). Because elasmobranchs do not have a

larval phase, their ability to disperse and colonise or re-colonise areas rests entirely on the movement behaviour of juveniles and adults.

Few studies have evaluated the use of closed areas as conservation tool for sharks (Knip *et al*., 2012). Prior to the implementation of a closed area it is vital to get an understanding of the site fidelity and movement behaviour of the species intended for protection (Barnett and Semmens, 2012) to ensure that an appropriate area is covered by the closed area (Speed *et al*., 2010; Field *et al*., 2011). However, the overall majority of global closed areas has been implemented opportunistically in the absence of rigorous management or conservation plans based on science (Hearn *et al*., 2010; Bond *et al*., 2012). Closed areas can be effective for highly resident (Bond *et al*., 2012) or mobile (Hearn *et al*., 2010) sharks, regardless of their size if they include a significant proportion of their home range (Barnett and Semmens, 2012; Knip *et al*., 2012). There are currently eight no-take MPAs in South Africa where M. mustelus are known to occur (Solano-Fernandez *et al*., 2012), but none were specifically designed to protect sharks. Langebaan Lagoon MPA (LMPA) is a small closed area situated inside Saldana Bay, a coastal embayment on South Africa's West Coast. Landlocked on three sides, the closed area provides an ideal opportunity to study residency of sharks within a no-take reserve. No-take MPAs will be referred to as closed areas.

For some species such as *C. limbatus* juveniles frequent well-defined nursery areas (Heupel and Hueter, 2002). There has been increased focus on identifying shark nurseries as essential habitat with the push towards developing closed areas at established nursery areas to protect juvenile sharks (Bonfil, 1999; Kinney and Simpfendorfer, 2009). This has not been practical for wide ranging species (Kinney and Simpfendorfer, 2009) and such nursery area closed areas have seldom been implemented (Bonfil, 1999; Heupel and Simpfendorfer, 2005b).

Additionally, for some species a fishery focused on younger age-classes such as the Australian Southern shark fishery on *M. antarcticus* has proven to be sustainable as long as other size classes are protected (Walker, 1998; Prince 2005; Kinney and Simpfendorfer, 2009). The protection of shark nursery grounds in absence of other fisheries management strategies may not conserve shark populations on their own, but they remain an important component of broader successful management plans (Kinney and Simpfendorfer, 2009). Although the protection of smaller age-classes may not be the most effective fishery management strategy for some species, the existence of a nursery ground within a closed area may provide additional protection to the juveniles of a small portion of a population. Additionally, the existence of a nursery ground within a prospective or existing closed area may provide political incentive through public concern to close area or enforce closure.

In this study, the movement behaviour of *Mustelus mustelus* in and around the closed area was investigated and the proportion of time spent in the different areas over a period of two years was quantified to evaluate the role of fishery closures in the conservation and management of this species. *Mustelus mustelus* is a small, benthic species, which is commercially fished throughout its range, where they sometimes provide an alternative target in the absence of high value teleosts (eg. Constantini *et al.*, 2000; da Silva, 2007; Saidi *et al.*, 2008). Although considerable movement of up to 1404 km has been reported (Mann and Bullen, 2009), conventional tagging studies in South Africa have shown that most *M. mustelus* were recaptured close to their release site, regardless of time at liberty (Mann and Bullen 2009). Based on tag and recapture information (Mann and Bullen 2009), I hypothesized that these sharks are resident within this small area and therefore potentially benefit from protection by the Langebaan Lagoon MPA. Additionally, the possibility that the closed area is a nursery ground for *M. mustelus* was investigated by applying the criteria

developed by Heupel *et al.*, 2007 that newborn or young-of-the-year sharks are more commonly found within the closed area than outside, that they remain within the closed area for extended periods of time and when they leave they often return, and that the area is repeatedly used across years.

MATERIALS AND METHODS

Study area

Saldanha Bay is a cool temperate coastal embayment situated on the west coast of South Africa (Fig. 3.1). Langebaan Lagoon (~135 km^2), the innermost part of Saldanha Bay, is a shallow, sheltered area. Large parts of the lagoon consist of sandbanks < 2 m deep, some of which are exposed at low tide (Kerwath *et al*., 2009). The sandbanks are separated by a branching channel between 5 and 11 m deep. Whereas the northern half of Langebaan Lagoon and the rest of Saldanha Bay are utilized by recreational and commercial fishers, the Langebaan Lagoon Marine Protected Area (34 km^2), in the southern part of the lagoon excludes fishing (Fig. 3.1).

Receiver placement

Twenty-eight acoustic receivers (VR2, VEMCO Ltd., Halifax) were moored at strategic positions throughout the bay in 2005 (Kerwath *et al*., 2009) (Fig. 3.1). When sharks passed through the detection range of a receiver, time and tag identification number were recorded. Double receiver lines were placed at the entrance of Saldanha Bay (area 1) and the closed area boundary (area 3) to ensure that the directions of fish movements were recorded (Thorstad *et al*., 2000; Kerwath *et al*., 2009). In addition, acoustic receivers were placed at positions in the fishing area (area 2) and also along the deep bifurcating channel within the closed area (area 4) (Figure 3.1). The detection range of the receivers within the closed area

was typically between 100 m and 200 m, but varied between 100 m and 400 m (Kerwath *et al*., 2009). Similarly, the detection range in the mouth of Saldanha Bay was typically 200 m, but varied between 50 m and 300 m, dependent on sea conditions, tide and location (Kerwath *et al*., 2009).

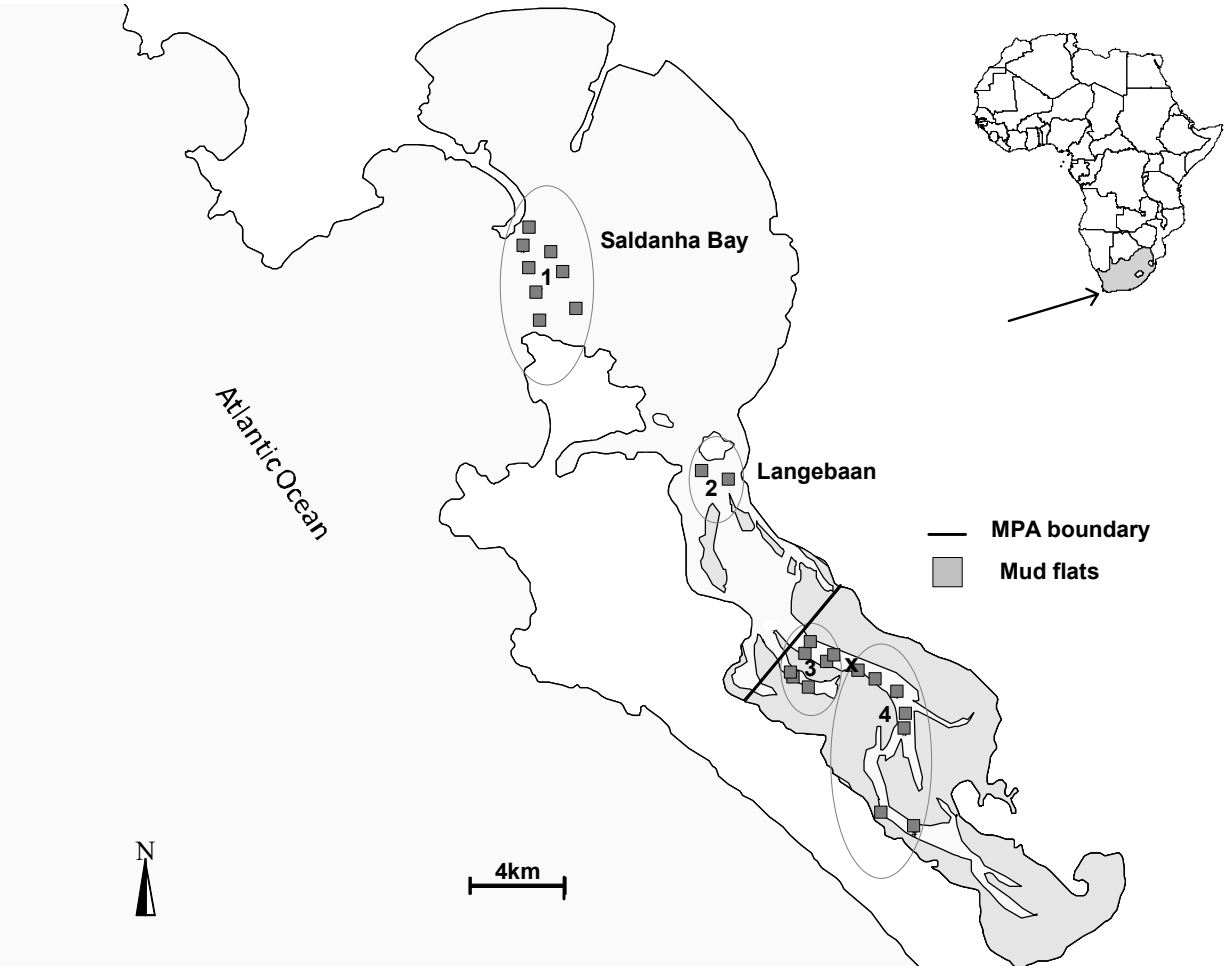


Figure 3.1. Saldanha Bay on the west coast of South Africa and its southern extension, the Langebaan Lagoon, which includes the closed area. Small grey squares denote individual receiver positions within the four receiver areas (1-4, indicated by grey circles). The grey shaded area within the closed area boundary represents sandbanks shallower than 2 m deep. Catch and release positions are denoted by x.

Shark capture and tagging

Twenty-four *M. mustelus* sharks, 12 females and 12 males (81-147 cm total length), were captured by rod and line between the 8th November and 10th November 2006 with baited circle hooks. Captured sharks were measured, sexed and released within the closed area after release condition was assessed (Tables 3.1 – 3.2, Figure 3.1.). They were anaesthetized by immersion in a seawater solution of phenoxyethanol (0.6 ml l^{-1}). Individually coded acoustic transmitters (VEMCO Ltd., Halifax, model V9-2L-R256, 69 KHz, random pulse rate 20 - 60 s) were implanted into the body cavity via a 1-2 cm incision in the abdominal wall using the methods described by Finstad *et al*., (2005). The surgery was accomplished within 2-5 minutes, during which water was sprayed over the gills. Sharks were placed in a recovery container until they recovered from anesthetization. Based on previous studies, battery life was expected to last for over one year (Kerwath *et al*., 2009; Hedger *et al*., 2010).

The maturity stage of males was determined by the state of the clasper. Males with claspers longer than the anal fin, calcified and able to articulate, were considered mature (Watson and Smale, 1998). The maturity of females was determined probabilistically using a length-maturity relationship and estimated at 1194 mm TL (Chapter 2).

Table 3.1. Size, maturity, release date, date of last detection and tracking period for female *M. mustelus* tagged with acoustic transmitters. Dataset represent the data used for analyses, dataset 1 indicates data between 1st November 2006 and 1st November 2007, dataset 2 indicates data from the 1st November 2006 to the 1st November 2008.

Shark ID	Total length (mm)	Maturity	Release date	Last detection date	Tracking period (days)	Dataset
l	810	Immature	2006/11/09	2008/11/25	747	1,2
m	849	Immature	2006/11/09	2008/11/25	747	1,2
e	875	Immature	2006/11/09	2008/04/15	523	1
f	950	Immature	2006/11/09	2008/07/14	613	1
j	1226	Mature	2006/11/09	2008/10/23	714	1
g	1302	Mature	2006/11/09	2008/02/19	467	1
d	1395	Mature	2006/11/09	2008/01/24	441	1
k	1474	Mature	2006/11/09	2008/11/22	744	1,2
Average	1117				494	

Table 3.2. Size, maturity, release date, date of last detection and tracking period for male *M. mustelus* tagged with acoustic transmitters. Dataset represent the data used for analyses, dataset 1 indicates data between 1st November 2006 and 1st November 2007, dataset 2 indicates data from the 1st November 2006 to the 1st November 2008.

Shark ID	Total length (mm)	Maturity	Release date	Last detection date	Tracking period (days)	Dataset
a	817	Immature	2006/11/08	2008/11/25	748	1,2
b	970	Immature	2006/11/08	2008/07/02	602	1
h	1003	Mature	2006/11/09	2008/11/25	747	1,2
c	1030	Mature	2006/11/08	2008/11/13	736	1,2
n	1098	Mature	2006/11/09	2008/11/25	747	1,2
o	1126	Mature	2006/11/10	2008/11/24	745	1,2
i	1135	Mature	2006/11/09	2008/11/25	747	1,2
Average	1082				473	

Studies on other small demersal sharks including *Mustelus canis* and *Scyliorhinus stellaris* demonstrated that it may take around 24 hours for animals to recover from exhaustive activity (Holeton and Heisler, 1978; Barham and Schwartz, 1992). However, as the physiological consequence of capture stress and wound recovery time is poorly understood (Skomal, 2007) data from the first seven days after tagging were removed from the analysis to avoid any abnormal behaviour related to capture and handling.

Duration of recording

To standardize datasets only sharks recorded for at least one annual cycle were included in the quantitative analyses. Eight sharks were monitored for less than one year. Two of these were only recorded within the first two weeks and did not cross the closed area boundary. Two other sharks were recorded within the first two months and also did not cross the closed area boundary. Of the four remaining sharks recorded for less than one year, although all were included inside the Saldanha embayment, two were last recorded within the closed area (after 160 and 187 days respectively), and two were last recorded outside the closed area (78 and 338 days respectively). I assume that these either died in areas without receiver coverage, were predated, that the transmitters failed, or that animals left the system but were not detected due to multiple signal collision. One more individual was removed from the analysis because it was not detected during the first year although it did subsequently return. These are not included in Tables 3.1 and 3.2. The remaining 15 transmitters exceeded the battery life and were detected for a period exceeding one year. The longest battery-life of any transmitter was 748 days (Tables 3.1 – 3.2). Nine sharks were recorded after two years, after which the receivers were removed from the study site (November 2008).

Data treatment

Raw telemetry data were standardised to hourly intervals. A shark was considered present at a particular receiver site if it had been detected at least once during that hour. In case sharks were detected simultaneously by neighboring receivers with overlapping detection ranges, the position was assigned to the receiver with the majority of detections within that hour. In the case of a tie, the receiver that first detected the shark was selected. The resulting standardized data consisted of a sequential set of positions per shark per hour. In addition, presence and absence from the closed area was logged every hour. During hours when a shark was not detected, no position was assigned, but presence (or absence) from the closed area was still determined in the following manner: Sharks that were present inside the closed area before and after the no-detection period were regarded as being inside the closed area. Sharks detected by the receiver line closed to the closed area boundary (area 3) and thereafter by no other receiver inside the closed area were logged as absent from the closed area. On rare occasions when sharks moved from inside to outside or vice versa without being detected at the boundary, positions were assigned as "unknown" and the number of hours was divided equally between presence and absence from closed area. In addition, closed area boundary crossings were counted and logged for each shark as it crossed from the closed area to outside and vice versa.

Data analysis

The telemetry data standardized to hourly intervals were divided into two different datasets: Dataset 1 contained data from the 15 sharks that were present in the system for at least one full year, from the 1st November 2006 to the 1st November 2007. Dataset 2, from the 1st November 2006 to the 1st November 2008, included only the nine sharks that were still present after two years, at the end of the study (Figure 3.2). The hourly intervals were

counted for each shark to determine the proportion of time spent inside or outside the MPA. The high mobility of sharks, as evidenced by movements exceeding 10 km in 20 minutes suggest to me that the extent of autocorrelation was negligible at a one hour bin size.

The number of individual sharks detected per day per receiver was calculated and plotted separately for both datasets to visualize the area utilisation across the study area over the study period. Dataset 1 was used to test for possible effects of shark size and sex on closed area utilisation patterns, namely the proportion of time spent inside the closed area and the number of crossings of its boundary. Data describing the proportion of time in hours that sharks spent inside the closed area were arcsine transformed to meet assumptions of normality. The effect of sex, maturity and size (TL mm) on proportion of time in hours spent inside the reserve was tested with a linear regression.

The centre of activity in terms of determining the receivers with the highest number of detections exhibited by individual sharks was calculated hourly with the use of receiver coordinates as a proxy of shark location. Hours when a shark was not detected and therefore without a position assigned was removed. The distance (km) between consecutive centers of activity was calculated to determine activity space. Numbers of individual shark present per receiver position were plotted by day.

Temporal patterns on closed area utilisation

The influence of diel cycles, season and year on the presence of sharks inside the closed area and the probability of sharks crossing its boundaries were examined using Generalised Linear Modeling. The models were applied to both datasets. A backward stepwise logistic regression analysis of binary response data (i.e. 1 or 0) was conducted in ‘R’ (R development Core

Team 2008; http:///CRAN.R-project.org/) to determine if there were differences between the response variables (a) presence in the closed area and (b) crossing the closed area boundary that can be explained by the predictor variables *season* (summer :December – February, autumn: March – May, winter :June – August and spring: September to November) and *diel period* (day, night, dawn and dusk). The predictor variable y*ear* (2007 and 2008) was added for dataset 2. Because hourly data for presence inside the closed area and crossings of the closed area boundary were available in binary format, a logit-link function was used to estimate the expected value of $\hat{p}$ such that:

$$logit\ (p) = \beta_0 + \beta_1 X_1 + \cdots + \beta_n X_n \quad [1]$$

where p represented the probability of a shark being found within the closed area or the probability of a boundary crossing. X_i are covariates with an estimated coefficient β, and a number n of applicable predictor variables.

Therefore, the probability of the presence of a shark in the closed area was expressed as:

$$logit\ (p) = \beta_0 + \beta_1(season) + \beta_2(dielperiod) + \beta_3(year) \quad [2]$$

The probability of a boundary crossing was expressed as:

$$logit\ (p) = \beta_0 + \beta_1(season) + \beta_2(dielperiod) + \beta_3(year) \quad [3]$$

The GLMs could not be applied to analyse movements out of Saldanha Bay due to the small number of detections at receiver location one. Instead, detections in this area were individually examined. Due to the overlapping receiver ranges, it was assumed that there was a high likelihood that sharks would be recorded whilst leaving or entering Saldanha Bay. Sharks were classified as having left the Saldanha Bay if they were recorded on the outside receiver line at area 1 (Fig. 3.1) and again recorded on the outside receiver line after a period of 24 hours without being recorded by the inner receiver line at this location.

RESULTS

General Sampling, receiver coverage and general movement patterns

A total of 24 sharks were captured and tagged, the total length of females ranged between 810 mm TL and 1470 mm TL (n = 12, average = 1170 mm TL), males ranged between 820 mm TL and 1360 mm TL (n = 12, average = 1082 mm TL) (Tables 3.1-3.2). Sharks sampled in Langebaan ranged between 381 mm TL to 1734 mm TL for females and 464 mm TL to 1267 mm TL (Chapter 2). Telemetered *M. mustelus* therefore are not representative of the population inside the lagoon. Since female and male *M. mustelus* reach 50 % maturity at 1194 mm TL and 967.44 mm TL respectively (Chapter 2), sharks chosen for telemetry ranged from maturing to adult. Due to sample selection, there was no significant difference in body length between males and females (t-test, n = 24, t = 0.67, p = 0.52).

The detection range of the receiver array did not cover the entire study area, the mean number of sharks recorded per day was lower than the total number of tagged sharks and not all sharks were recorded on every day (Figure 3.2; Tables 3.1-3.2). Sharks were recorded at multiple positions on some occasions within the same hour, but they were on no occasion recorded by receivers located inside (area 4) and outside the reserve (areas 1 and 2) within the same hour. Detections within the array were not distributed equally over time and among receivers (Figure 3.3). Receivers within the closed area (area 4) detected the presence of individual sharks more frequently than receivers at areas 1 and 2 for both datasets.

During the entire study period, only eight sharks were recorded by receivers in area 1 at the Saldanha Bay mouth (~15 km from the release site), whereas 14 sharks were detected at the southern-most receivers inside the closed area (area 4, ~3 km from the release site). Seven

individuals were recorded on both the southern-most (4) and the northernmost receiver area (1), which were 16 km apart.

Sharks were concentrated inside receiver area 3 and 4, with limited movement into receiver areas 1 and 2 in summer and autumn, during winter and spring sharks were spread out throughout the system (Figure 3.3). This represented a consistent seasonal pattern as this was represented during two consecutive years.

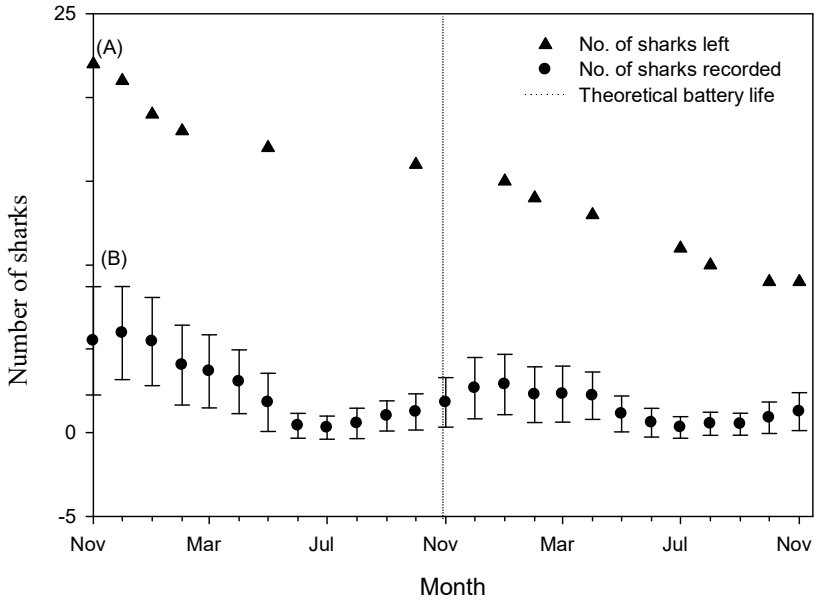


Figure 3.2. Average number of *M. mustelus* recorded per day for each month (black circles), with error bars representing the standard deviation. The solid triangles represent the total number of sharks in the study area during that period.

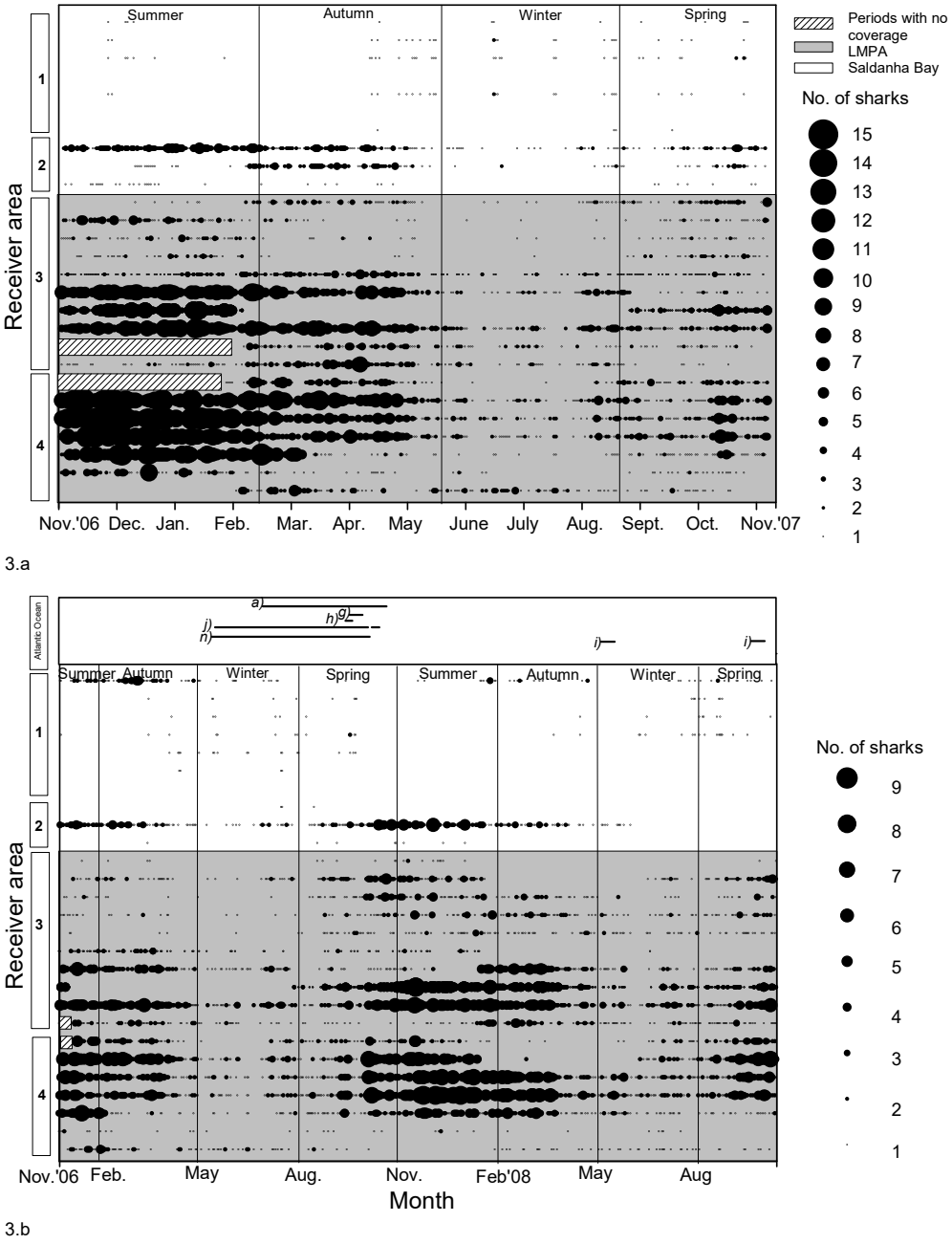


Figure 3.3. The number of acoustically tagged sharks recorded per day at each of the 28 receivers during November 2006 and November 2007 (3.a, dataset 1, n = 15) and during November 2006 and November 2008 (3.b, dataset 2, n = 9). Receiver areas (see Fig. 3.1) are denoted on the left side of the graph. Periods when excursions into the Atlantic Ocean occurred are indicated on the top panel of 3.b. Only shark *a*, *g*, *h*, *i*, *j* and *n* left Saldanha Bay during both study periods (shark *i* and *j* left twice, the others once).

Eight individuals were recorded at the Saldanha Bay mouth, of which only six left the bay and ventured into the Atlantic Ocean for durations ranging from two to 157 days (median = 111 days, Fig.3.3). Four sharks left the embayment only once during 2007 (shark *a* left on the 4 July for 112 days, shark *g* left on the 20 September for 10 days, shark *h* left on the 14 September for two days and shark *n* left on the 12 May for 157 days) and one shark (*j*) left twice (left on the 19 May for 139 days and left on the 5 October for 5 days, Fig.3.3). Only one shark (*i*) left the bay in 2008 but did so on two separate occasions, once during winter (left on the 6 May for 10 days) and once during spring (left on the 19 September for 13 days). All six sharks returned and remained in the bay until the receivers were removed in 2008. Movements out of Saldanha Bay occurred during the Austral winter (May and July) and spring (September and October). Movements out of the bay in winter (mean = 103.75 days, range = 10 – 156 days, SD = 65.18) were generally longer than those in spring (mean = 6.75 days, range = 2 – 13 days, SD = 5.62) with animals generally returning in spring/ summer months.

Within the first study year, sharks (n = 15) spent more time inside the closed area than outside (mean = 79 %, range = 44-100 %, SD = 21 %). Within the first year two sharks never left the closed area, while the remaining sharks (n = 13) frequently crossed into the fishing area (mean number of crossings per individual = 40, range = 0 – 163, SD = 51. 16) throughout the period. Within the second year only one shark never left the closed area, similarly the remaining sharks (n = 7) frequently crossed the fishing area (mean number of crossings per individual = 51, range = 1 – 158, SD = 53.19).

There was no significant difference in proportion of time spent inside the closed area between males and females (Linear Regression, n = 15, $R^2 = 0.58$, p = 0.06). There was also no

significant difference between proportion of time spent inside the closed area and size of shark (TL mm) (Linear Regression, n = 15, $R^2 = 0.58$, p = 0.06). Immature sharks spent a significantly larger proportion of time inside the closed area than mature sharks (Linear Regression, n = 15, $R^2 = 0.58$, **p = 0.03**). The addition of maturity stage to the model explained 25% of the deviance of the model.

Table 3.3 lists all the results of the models for the predictor variables *season*, *diel period* and *year* for datasets one and two. For the 15 sharks considered in dataset 1, *season* had the biggest effect on the proportion of time sharks spent inside the closed area (mean = 0.30, range 0.04-0.53, SD 0.17), but the proportion of deviance explained by *season* varied considerably among individuals. For the nine sharks in dataset 2, the predictor *season* was still significant, but had less explanatory power than for dataset 1 (mean proportion of time spent inside the closed area = 0.17, range = 0.06-0.39, SD = 0.12, Table 3.3). The explanatory variable *season* only showed a significant response for all sharks (100 %) in dataset 1 (n = 12) and dataset 2 (n = 8) that had enough data for testing (Table 3.3). Seasonal influence on presence inside the closed area was significant with high proportion of deviance explained for sharks that migrated out of Saldanha bay (shark I.D. $a = 0.48$, $g = 0.49$, $i = 0.53$, $j = 0.39$, and $n = 0.31$, Table 3.3), although there was also a strong seasonal component for other individuals. For dataset 1 higher numbers of sharks were found inside the closed area per time interval in summer (average number of sharks inside the closed area per time interval = 13.50, range = 9 - 15, SD = 1.20), followed by autumn (average number of sharks inside the closed area per time interval = 12.94, range = 8 - 15, SD = 1.67), winter (average number of sharks inside the closed area per time interval = 9.61, range = 7 - 11, SD = 0.82) and lastly spring (average number of sharks inside the closed area per time interval = 9.46, range = 0 - 15, SD = 2.71). For dataset 2 higher number of sharks were found inside the closed area per

time interval in summer (average number of sharks inside the closed area per time interval = 8.03, range = 3 - 9, SD = 1.02), followed by autumn (average number of sharks inside the closed area per time interval = 8.00, range = 4 - 9, SD = 1.07), spring (average number of sharks inside the closed area per time interval = 6.68, range = 3 - 9, SD = 1.44), and lastly winter (average number of sharks inside the closed area per time interval = 6.25, range = 4 - 7, SD = 0.62).

Diel period explained < 1% of the deviance of the model for both datasets. For dataset 1, diel period was significant for 31 % of individuals in dataset 1 and 63 % of individuals in dataset 2. All sharks with significant responses to *diel period* had a marginally higher fraction (<0.01) of time spent inside the closed area during daytime hours. For dataset 1, a high number of sharks were found inside the closed area per time interval during dawn (average number of sharks inside the closed area per time interval = 11.48, range = 0 - 15, SD = 2.58), followed by day (average number of sharks inside the closed area per time interval = 11.40, range = 0 - 15, SD = 2.56), night (average number of sharks inside the closed area per time interval = 11.36, range = 0 - 15, SD = 2.56) and lastly dusk (average number of sharks inside the closed area per time interval = 11.17, range = 0 - 15, SD = 2.48). For dataset 2, higher number of sharks were found inside the closed area per time interval during dawn (average number of sharks inside the closed area per time interval = 7.34, range = 3 - 9, SD = 1.35) followed by day (average number of sharks inside the closed area per time interval = 7.30, range = 3 - 9, SD = 1.35), night (average number of sharks inside the closed area per time interval = 7.20, range = 3 - 9, SD = 1.32) and lastly dusk (average number of sharks inside the closed area per time interval = 7.14, range = 3 - 9, SD = 1.31).

The predictor variable *year,* which was included in the model for dataset 2, was significant for all sharks and on average explained a higher proportion of deviance than *diel period* and *season.* During 2007 and 2008, the sharks spent an average of 74 % (range = 44-100 %, SD = 21) and 80 % (range = 51-100 %, SD = 20) of the time inside the closed area, respectively. For dataset 2 higher number of sharks were found inside the closed area per time interval in 2008 (average number of sharks inside the closed area per time interval = 7.32, range = 3 - 9, SD = 1.36) than 2007 (average number of sharks inside the closed area per time interval = 7.18, range = 3 - 9, SD = 1.29).

During the 2007 study period the average daily activity space of individuals ranged from 0.45 to 1.18 km^2. The majority of average daily activity space values were < 1 km^2 (89 %), whilst 44 % of average daily activity space was < 0.5km^2. Monthly mean estimates ranged from 0.44 to 1.66 km^2 for all individuals. The majority of the average monthly activity space values occurring below 1 km^2 (63 %), whilst 32 % of average monthly activity space occurred below 0.5 km^2.

Table 3.3. Presence in the closed area: results from logistic regression models, showing the p-values (P) and proportion of deviance (P-Dev) explained by the predictors season and diel period (dawn, day, dusk, night) to the response variable presence in closed area for *M. mustelus* that were present in both datasets (n = 15 for dataset 1 and n = 9 for dataset 2). Dash denotes sharks that did not spend any time outside the reserve or less than 1 % of time was spent outside the closed area. * denote values that were significant at a 0.05 level.

	Dataset 1				Dataset 2					
Shark ID.	Season		Diel Period		Season		Diel Period		Year	
	P	P-Dev	P	P-Dev	P	P-Dev	P	P-Dev	P	P-Dev
a	<0.001*	0.48	0.25	<0.01	<0.001*	0.30	0.05	<0.01	<0.001*	0.26
b	<0.001*	0.25	0.88	<0.01						
c	<0.001*	0.51	0.65	<0.01	<0.001*	0.09	<0.001*	<0.01	<0.001*	<0.01
d	-	-	-	-						
e	<0.001*	0.09	<0.001*	<0.01						
f	<0.001*	0.14	0.12	<0.01						
g	<0.001*	0.49	0.79	<0.01						
h	<0.001*	0.10	<0.001*	<0.01	<0.001*	0.06	0.12	<0.01	<0.001*	0.09
i	<0.001*	0.53	<0.001*	<0.01	<0.001*	0.39	<0.001*	<0.01	<0.001*	0.55
j	<0.001*	0.39	<0.001*	<0.01						
k	-	0.26	0.23	<0.01	<0.001*	0.11	<0.001*	<0.01	<0.001*	0.10
l	-	-	-	-	-	-	-	-	-	-
m	<0.001*	0.28	0.17	<0.01	<0.001*	0.20	0.88	<0.01	<0.001*	0.21
n	<0.001*	0.31	0.62	<0.01	<0.001*	0.06	<0.001*	<0.01	<0.001*	0.09
o	<0.001*	0.04	0.93	<0.01	<0.001*	0.16	<0.001*	<0.01	<0.001*	0.12

Crossing the closed area boundary

The explanatory variables *season, diel period* and *year* explained little of the variation in the number of crossings of the closed area boundary per individual. The explanatory variable *season* showed a significant response for 53 % of sharks in dataset 1 and 77 % of sharks in dataset 2 (Table 3.4). This variable explained less than 1 % of the variance for all sharks in

dataset 1. In dataset 2 this explanatory variable explained an average of < 1 % of the deviance (range = 0.03 – 0.22, SD = 0.065). For dataset 1, greater numbers of sharks crossed the closed area boundary per time interval in summer (average number of crossings = 2.81, range = 0 - 11, SD = 1.94), followed by spring (average number of crossings = 0.87, range = 0 - 11, SD = 1.43), autumn (average number of crossings = 1.29, range = 0 - 6, SD = 1.16), and lastly winter (average number of crossings = 0.28, range = 0 – 3, SD = 0.62). For dataset 2, higher numbers of sharks crossed the closed area boundary per time interval in summer (average number of crossings = 0.09, range = 0 - 3, SD = 0.31), followed by autumn (average number of crossings = 0.04, range = 0 - 2, SD = 0.20), spring (average number of crossings = 0.01, range = 0 - 2, SD = 0.12), and lastly winter (average number of crossings = 0.01, range = 0 - 1, SD = 0.09). Although the predictor *diel period* was significant for 30 % and 44 % of the animals in dataset 1 and 2, respectively, the overall proportion of deviance explained by the model was negligible (Table 3.4). For dataset 1 the variable *diel period* explained an average of 0.02 proportion of the deviance (range = 0.01 – 0.08, SD = 0.02). For dataset 2 this variable explained an average of 0.02 proportion of the deviance (range = 0.01 - 0.04, SD = 0.01). Overall, no clear diel pattern was evident. For dataset 1 higher numbers of sharks crossed the closed area boundary per time interval in *dawn* (average number of crossings = 1.38, range = 0 - 11, SD = 1.76), followed by *day* (average number of crossings = 1.37, range = 0 - 10, SD = 1.69), *dusk* (average number of crossings = 1.26, range = 0 - 8, SD = 1.5) and lastly *night* (average number of crossings = 1.23, range = 0 - 10, SD = 1.61), and For dataset 2 higher numbers of sharks crossed the closed area boundary per time interval in *night* (average number of crossings = 0.04, range = 0 - 3, SD = 0.22), followed by *dusk* (average number of crossings = 0.04, range = 0 - 2, SD = 0.19), while *dawn* (average number of crossings = 0.03, range = 0 - 2, SD = 0.18) and *day* (average number of crossings = 0.03, range = 0 - 2, SD = 0.16) were similar. *Year* as an explanatory variable was only significant

in 33 % of the individuals. The addition of this variable only explained an average of 0.04 proportion of the deviance (range = <0.01 – 0.09, SD = 0.03). For dataset 2 more average crossings for all sharks combined per time interval were observed during 2007 (average number of crossings = 0.05, range = 0 - 3, SD = 0.23) than 2008 (average number of crossings = 0.02, range = 0 - 2, SD = 0.13). As data was only received from 15 (dataset 1) and 9 (dataset 2) of 24 telemetered sharks and these did not represent the full-size range within the lagoon (Chapter 2), the proportion of time spent inside and outside the closed area was not evaluated for size or sex.

Table 3.4. Crossings of the closed area boundary: Results from the logistic regression models, showing the showing the p-values (P) and proportion of deviance (P-Dev) explained by the predictors season and day period (dawn, day, dusk, night) and year (b) to the response variable crossings for *M. mustelus* that were present a) until the end of 2007 (dataset 1; n = 15), and b) until the end of 2008 (dataset 2; n = 9). Dashes denote sharks that did not spend any time outside the reserve or less than 1% of movements represented crossing and therefore there was too little data to run GLM. * denote P-values that were significant at a 0.05 level.

	Dataset 1 a)				Dataset 2 b)					
Shark	Season		Diel Period		Season		Diel Period		Year	
ID	Pv	P-Dev	Pv	P-Dev	Pv	P-Dev	Pv	P-Dev	Pv	P-Dev
a	0.52	<0.01	0.22	<0.01	<0.001*	0.06	0.66	<0.01	0.60	<0.01
b	0.42	<0.01	0.58	<0.01						
c	0.39	<0.01	0.58	<0.01	-	-	-	-	-	-
d	-	-	-	-						
e	-	-	-	-						
f	-	-	-	-						
g	0.04*	<0.01	0.04*	<0.01						
h	<0.001*	<0.01	<0.001*	<0.01	<0.001*	0.05	<0.001*	0.01	<0.001*	0.07
i	<0.001*	<0.01	<0.001*	0.08	<0.001*	0.09	<0.001*	0.04	0.11	<0.01
j	<0.001*	<0.01	0.08	<0.01						
k	<0.001*	<0.01	0.62	<0.01	<0.001*	0.22	0.66	<0.01	<0.001*	0.09
l	-	-	-	-	-	-	-	-	-	-
m	<0.001*	<0.01	0.31	0.02	<0.001*	0.04	0.01*	0.03	0.20	<0.01
n	<0.001*	<0.01	<0.001*	0.03	<0.001*	0.11	<0.001*	0.03	0.08	<0.01
o	<0.001*	<0.01	<0.001*	0.02	<0.001*	0.03	0.05	<0.01	<0.001*	0.04

DISCUSSION

General movement patterns inside and out of Saldanha Bay

The results of this study showed that *M. mustelus* were resident within Saldanha Bay over prolonged periods, but occasionally migrated or extended their range out into the Atlantic Ocean for brief periods. *M. mustelus* show extreme residency especially within the closed area inside Langebaan Lagoon with occasional forays outside this area. Site fidelity has been commonly documented in many shark species (Heupel *et al*., 2004; Simpfendorfer *et al.*, 2005; Speed *et al.*, 2010). The repeated movements of sharks across wide areas suggest that these animals are familiar with the area and are able to navigate between preferred sites (Papastamatiou *et al*., 2011). Within the bay, *M. mustelus* spent much of the time in the southern part of the bay characterised by shallow sandbanks, as opposed to the deeper areas in the northern part of the bay. Average daily movements from analysis of activity space and based on what is known of prey sources in the Lagoon (Puttick, 1977) were generally less than 1 km^2 in these areas, and most likely represented foraging behaviour between preferred high-density prey areas. However, the receiver coordinates were used as a proxy of shark location. In reality sharks detected in the array were typically within 100-200 m of the receiver location given its reception range (Kerwath *et al*., 2009). Therefore, there was an error associated with average daily movements and center of activity calculations that is characteristic of all telemetry studies using acoustic arrays.

Residency within a small area (< 1 km) even given reception range of this array was similar to what was found for *M. californicus* (Espinoza *et al.*, 2011). High densities of the prawns *Callianassa kraussii* and *Upogebia africana*, and crab *Hymenosoma obiculare,* all important prey of *M. mustelus*, are found in these shallow areas (Wynberg and Branch, 1991), which suggests that the distribution of *M. mustelus* might be partially linked to the distribution of

their prey, as has been found with other shark species (Sims *et al.*, 2008). This study shows that immature sharks showed a higher degree of residency inside the closed area.

Whilst foraging on the sandbanks, sharks were likely out of range of the receivers since these were moored along the channels. Prolonged outings onto the sandbanks would also explain the relatively low number of daily detections of individual sharks compared with the actual number of individuals that were still in the system. The utilisation of shallow areas could also be linked to predator avoidance behaviour or thermoregulation. Sharks and other fishes have been shown to move into shallower water in order to avoid intra- and interspecific predation (Fraser and Cerri, 1982; Morrissey and Gruber, 1993a, b), although on the contrary it has also been shown that prey species may avoid shallow areas (Heithaus *et al.*, 2002, 2006; Barnett and Semmens, 2012). Large predators such as *Notorynchus cepedianus* and *Carcharhinus brachyurus* make occasional forays into the Lagoon (da Silva, unpublished catch data), but are unlikely to move onto these sandbanks as they are shallower than 2 m deep and partly exposed during low tide. *M. mustelus* could therefore receive protection from these predators while present on shallow sandbanks. Utilisation of shallow areas for behavioural thermoregulation benefits have been shown in a number of sharks including *N. brevirostris*, *T. semifasciata* and *C. melanopterus* (Hight and Lowe, 2007; Morrissey and Gruber, 1993a, b, Speed *et al*., 2012). *M. mustelus* could benefit from being present in shallow tidal banks through optimization of metabolic rates involved in growth, digestion and gestation (Morrissey and Gruber 1993a, b, Economakis and Lobel 1998; Digirolamo *et al*., 2012). Movement onto shallow banks could also be explained by a combination of the above factors.

Although sharks were present in the southern lagoon during the entire study, seasonal variation in area utilisation was evident. During autumn, winter and early spring, some sharks

dispersed more widely across the bay and beyond, whereas only a few outings beyond area 2 occurred during summer. This seasonal pattern might be linked to a general increase of prey *C. kraussi*, *U. africana*, and *Hymenosoma obiculare* on the shallow banks inside the lagoon in spring (Puttick, 1977). However, not all movements made by marine vertebrates and other animals are associated with optimal foraging (Sims, 2003). Animal movement behavior is a complex trade-off between optimal foraging, predator avoidance, access to reproduction and physiological constraints (Dingle, 1996). Water temperature changes have been shown to influence movement of Triakid sharks, including *Mustelus antarcticus*, *M. henlei* and (*M. californicus* (Hopkins and Cech, 2003; Espinoza *et al*., 2011; Barnett and Semmens, 2012). In the Saldanha Bay system, temperatures peak in the shallow areas in summer, which might offer thermal advantages (Lowe and Goldman, 2001) such as increased growth (Hight and Lowe, 2007) and decreased gestation periods (Matern *et al.*, 2000).

The seasonal movement between the closed area and Saldanha Bay, and even out of Saldanha Bay, had a strong seasonal component and can be considered an annual migration as defined by Dingle (1996) as it occurred during a specific, predictable time period and included a return movement and was repeated in the second year of the study. However, most individuals did not move over a distance larger than 16 km (i.e., distance between the two most far away recordings). Although most of the sharks remained within Saldanha Bay, some individuals left the bay in spring and winter for the open Atlantic Ocean, before returning again to the protected area within the Langebaan Lagoon.

It is possible that the seasonal movements recorded were related to reproduction. *M. mustelus* are commonly found in shallow bays (Smale and Compagno, 1997) where they reproduce annually (Saidi *et al*., 2008) or possibly biennially (Smale and Compagno, 1997; Chapter 2).

M. mustelus ovulation, mating and parturition occur between October and December, with an 11-month gestation period (Chapter 2), these important life-history stages occur within the time periods where animals were concentrated inside the closed area. These crucial life-history stages also occurred around the times in spring after some individuals left the Saldanha Bay area for the Atlantic Ocean. Hence, the few individuals that left the Saldanha Bay in this period likely either did not reproduce that year, or they left the bay before pupping. Mature individuals that stayed inside the closed-area may have reproduced. However, the latter is unlikely since neonates were commonly caught inside the protection of the closed area (Chapter 2).

Sharks often move out of coastal areas over winter (Abrantes and Barnett, 2011; Barnett and Semmens, 2012). Although the reasons that *M. mustelus* left the Bay during winter are unknown, this may also be related to behavioural thermoregulation (to be examined in detail in Chapter 4), food availability or predator avoidance. Other studies have speculated that movement of *Mustelus* spp. is influenced by predator avoidance (Campos *et al*., 2009; Barnett *et al.*, 2010; Barnett and Semmens, 2012). Due to lack of data, this study was unable to determine if the movement *M. mustelus* at different temporal scales was affected by predators. No predators where included in the telemetry study, nor were bite marks or scarring from failed predation events observed. One single occasion of predation occurred during sampling (Chapter 2) when a large *C. brachyurus* (estimated at 2.5 m) predated on an approximately 1300 mm TL female whilst on the line (da Silva, unpublished data).

Movement in the closed area from a management perspective

MPAs with closed areas have been acknowledged as a possible conservation method for sharks in the absence of fishing regulations (Bonfil, 1999; Barker and Schleussel, 2005).

However, few studies have examined the movement patterns of sharks in relation to existing closed areas (e.g. Barnett *et al.*, 2011; Bond *et al.*, 2012b; Knip *et al.*, 2012). The results in this study in the Langebaan Lagoon MPA, hereafter referred to as closed area and surrounding Saldanha Bay show that closed areas may provide a significant amount of protection to the *M. mustelus*, since they spent a large proportion of the time (average 79 %) within the closed area, although the closed area represents only 35 % of the entire bay area (Kerwath *et al*., 2009).

With the exception of the six sharks that left Saldanha Bay during the study, the remaining sharks spent a large proportion of their time inside the closed area. Notwithstanding, the closed area did not represent total protection for the *M. mustelus*, except for a small fraction that stayed within the closed area all the time and never entered the fished area. Males and females seemed equally protected, as no differences in their movement behaviour were recorded. Seasonal movement occurred in the form of an expansion of range in winter and spring. The least protection was offered during winter, which was the period with the highest frequency of recordings outside the fished area. Moreover, *M. mustelus* were protected during their pupping period in spring (Department of Agriculture, Forestry and Fisheries, unpublished data). Neonates are commonly found inside, but not commonly outside closed area in spring (Department of Agriculture, Forestry and Fisheries, unpublished data), suggesting that this area represents a nursery ground where neonates are protected. Fishing inside Saldanha Bay is mostly restricted to summer (Kerwath *et al.,* 2009) and although *M. mustelus* are often released by recreational anglers, capture stress is known to increase mortality and predation, at least for other species (Skomal, 2007). *M. mustelus* are commercially fished in South Africa to supply the high demand for shark fillets in Australia (da Silva and Bürgener, 2007; da Silva *et al.*, 2015). Along with a suite of other sharks

including *Galeorhinus galeus* and Carcharhinidae they are targeted or caught as by-catch in the inshore trawl fishery, demersal shark longline fishery and the commercial rod and reel fishery (da Silva *et al.*, 2015). Although commercial fisheries are mainly targeting these sharks on the southern and eastern Cape Coasts in South Africa, occasional commercial fishing does occur on the western Cape Coast as well as substantial poaching (da Silva, 2007). The Langebaan Lagoon closed area is the only closed area in South Africa where the protection of *M. mustelus* has been investigated.

The fact that *M. mustelus* spent most of their time inside the closed area during peak fishing season in summer increases the conservation value of the closed area. According to the results in this study, *M. mustelus* in the closed area were therefore protected during their parturition period which coincides with peak fishing periods. During sampling for this study in Saldanha Bay and monitoring at fishing competitions frequently held in Langebaan neonate and juvenile sharks were seldom caught outside the closed area confines (da Silva, unpublished catch data, Department of Agriculture, Forestry and Fisheries, unpublished data). This suggests that higher concentrations of young sharks are found inside the closed area and that protection thereof is extended to neonate and juvenile sharks. To increase the level of protection offered by the closed area and Saldanha Bay area, fishing for *M. mustelus* could be restricted in winter, when they sharks disperse from the closed area. Lack of daily variation in habitat use indicates that fishing restrictions in certain times of the day will likely not increase the degree of protection.

A high degree of residency within the closed area was also found for two mobile marine teleost species; *Rhabdosargus globiceps* (Attwood *et al.*, 2007; Kerwath *et al.*, 2009) and *Pomatomus saltatrix* (Hedger *et al.*, 2010). The results of these studies showed frequent

crossings of the closed area boundary, a high proportion of time spent inside the closed area, and seasonally influenced movement. Therefore, the closed area provides protection for at least three commercially important species with different life-history characteristics.

The extent of animal movement between a protected and surrounding unprotected area is the major factor in determining the effectiveness of a closed area (Chapman *et al.*, 2005). Movement patterns and residency of highly mobile sharks around or in nursery grounds have been studied in some detail (Holland *et al.*, 1993; Ebert and Ebert, 2005), however, few authors have studied these in relation to protection provided by a closed area (Chapman *et al*., 2005; Heupel and Simpfendorfer, 2005; Garla *et al*., 2006a; Barnett *et al.*, 2011). A recent study by Knip *et al.*, (2012) investigated the degree of protection that closed areas within the Great Barrier Marine Park provide to juvenile *Carcharhinus amboinensis* and adult *C. sorrah*. These sharks spent a large proportion of the time inside the reserves (average 22 and 32 % of their time), similar to *M. mustelus* in the present study, although the residency of *M. mustelus* is considerably larger. Due to their size and size of the acoustic tags, the movement behaviour of newborn and juvenile sharks was not investigated in this study. It was shown in Chapter 2 that neonate and juvenile sharks are more commonly found within the LMPA than outside, and the scarcity of sharks outside the LMPA suggested that they remain inside for extended periods. Therefore, the nursery ground criteria as proposed by Heupel *et al.* (2007) was confirmed given the increased abundance and extended residency of *M. mustelus* inside the LMPA, their tendency return to the closed area once they leave, and the presence of neonates, juveniles and pregnant females within its confines.

In conclusion, the results show that if strategically placed, closed areas may be effective in protecting *M. mustelus* and species with similar life-history in the absence of species-specific management. Quantitative, long-term studies of the habitat use of exploited elasmobranchs during important life-history stages are vital to understand the degree of protection provided by closed areas.

CHAPTER 4: ENVIRONMENTAL EFFECTS ON MIGRATION, HABITAT USE AND FINE-SCALE MOVEMENT OF *MUSTELUS MUSTELUS*

ABSTRACT

The movement of *M. mustelus* in relation to environmental conditions was investigated at various temporal scales through the use of acoustic telemetry and temperature and depth transmitters (TDL) in the closed area of the Langebaan Lagoon Marine Protected Area. Twenty-four sharks were tagged with acoustic tags from 2007 to 2008. A number of generalised additive and generalised additive mixed models (GAMMs), were used to explain patterns of movement in terms of the environmental variables *absolute temperature*, *delta temperature* (rate of change of temperature), *tide*, *diel cycle* and *moon phase.* The most important environmental parameters affecting movement and direction of movement was *absolute temperature* and *delta temperature*. The movement of *M. mustelus* was not affected by tide and only minimally affected by the diel cycle. The movement of *M. mustelus* inside the Saldanha embayment was predominantly affected by temperature, suggesting behavioural thermoregulation. When the temperature increased, sharks tended to move into colder water, towards Saldanha Bay. The thermal preference for *M. mustelus* was between 18 and 22˚C as determined by GAMMs for environmental conditions experienced in summer. Males preferred cooler water than females for both summer and winter. In winter, immature sharks preferred warmer water than mature sharks, while in summer the opposite trend was observed. The combination of sheltered, warm waters and rich feeding grounds in conjunction with the protective effect of the closed area may explain the high abundance and regular occurrence of *M. mustelus* within the Langebaan Lagoon.

INTRODUCTION

Sharks are familiar with their habitat, can pinpoint foraging locations and locate areas and identify periods in which predators are likely to be absent (Papastamatiou *et al*., 2011; Sims *et al*., 2006a, 2008). By being aware of specific features within their habitat, they are able to reduce time searching for food and so conserve energy (Papastamatiou *et al*., 2011). Ultimate causes of movement are fundamental to survival and evolution of a species and include reproduction, growth, predator avoidance and feeding. Proximate causes of movement include those related to fluctuatating environmental conditions, but these do not directly impact survival, unless environmental variation is extreme and outside physiological tolerance (Matich and Heithaus, 2012).

Residency is the most common behaviour pattern among fishes (Gerking, 1953), presumably because the advantages of familiarity of terrain outweighs the costs of movement, the unpredictability of resources and the lack of immunity to new diseases. For example, *C. carcharias* are resident in False Bay, South Africa, but aggregate around the Cape fur seal colony at Seal Island to prey on young of the year seals (Kock *et al*., 2013), demonstrating both a knowledge of the location of food and an ability to navigate. Prey abundance and presence of predators typically fluctuate seasonally. The limited availability of the former and the increased presence of the latter would increase the perceived benefits of moving. Juvenile *Sphyrna lewini* (Holland *et al.*, 1993), *N. brevirostris* (Guttridge *et al*., 2012) and *C. limbatus* (Heupel and Hueter, 2002) select habitat primarily to avoid predators.

Fluctuations in environmental conditions can provide information about imminent changes in food and predator abundance. In addition, each species has its own set of physiological constraints that impacts their survival. Therefore, an ability to respond to environmental

change is required for reproduction and survival. Those animals with the ability to anticipate these changes and respond appropriately and rapidly are at an advantage (Dingle, 1996). Once conditions become less favourable, an appropriate response would be to find more acceptable conditions elsewhere. Environmental changes that provide information about habitat include direct influences such as those associated with tides, seasons, and photoperiod. These cause changes temperature, visibility, salinity, and oxygen (Dingle and Drake, 2007).

The habitat selected by a shark is determined by a complex of physical and biotic factors (Fréon and Misund, 1999), and can be selected by responses to abiotic factors such as temperature and salinity but also ecological factors such as prey availability and abundance of predators and competitors (Sims, 2003). Spatial distribution across this habitat may be determined by a single or combination of these factors (Heithaus *et al*., 2002). In cases where there are no predators and environmental conditions are stable, sharks generally select habitats with abundant high-quality resources to maximize energy inputs (Sims, 2003). For example, in the absence of predators juvenile *N. brevirostris* spend their time in high quality food environments. When predators arrive with the incoming high tide, they hide inside mangrove forests (Digirolamo *et al.*, 2012). The change in tide and consequent change in temperature, salinity or oxygen may provide a warning of the imminent arrival of these predators.

Movement under stable environmental conditions might also be induced by life-history events such as reproduction (Claramunt *et al.,* 2005; Schofield *et al.,* 2009). Whereas behaviour in response to rapidly fluctuating conditions is often irregular and chaotic, movement linked to life-history often occurs in the form of regular migration (Dingle and

Drake, 2007). Alternatively, many sharks undertake migrations or shift seasonal distribution in relation to predictable changes in seasonal environmental conditions (Wilson *et al.,* 2001; Hopkins and Cech, 2003; Grubbs *et al*., 2007; Espinoza *et al*., 2011). The distribution and abundance pattern of a species is determined by a complex combination of the life-history events and responses to environmental change.

The majority of elasmobranchs are poikilotherms and are forced to live within their thermal niche (Grubbs, 2010). Water temperature is therefore likely to an important factor (Grubbs, 2010) for movements at small (Hight and Lowe, 2007; Morrissey and Gruber, 1993a,b) and large scales (Hopkins and Cech, 2003). Juvenile *N. brevirostris* select shallow water greater than 30 ˚C to maintain optimal metabolic performance (Morrissey and Gruber, 1993a). On a larger scale, the seasonal movement of *Myliobatis californica*, *Triakis semifasciata* and *Mustelus henlei* in Tomales Bay, California, is driven by temperature. These shark species leave the bay in autumn as water temperature falls below 10 ˚C, but return in spring after water temperature rises (Hopkins and Cech, 2003).

In temperate areas, the photoperiod is the most reliable predictor of seasonal change (Dingle, 1996). Elasmobranchs commonly occupy different diurnal and nocturnal temporal areas, often increasing their activity at night (Ackerman *et al*., 2000; Gruber *et al.*, 1988; Holland *et al.*, 1992; Vaudo and Lowe, 2006). Diel behaviour has been observed in temperate species that occupy deeper water during the day and move close inshore or shallower at night, such as sixgill sharks *Hexanchus griseus* (Andrews *et al.*, 2009) and soupfin sharks *Galeorhinus galeus* (West and Stevens 2001). Distinct diel pattern has also been observed for tropical species; nocturnal expansions of area usage are typical of shallow water species with distinct home ranges, such as *Sphyrna lewini* (Klimley and Nelson, 1984; Klimley *et al*., 1988),

Triaenodon obesus (Barnett *et al.*, 2012), *Triakis semifasciata* (Hight and Lowe 2007), *Dasyatis lata* (Cartamil *et al.*, 2003) and *Manta birostris* (Dewar *et al*., 2008). These home range expansions are usually a result of balancing optimal foraging, predator avoidance and energy conservation.

Several studies have examined the movement of Triakid sharks in relation to environmental conditions. Generally, the spatio-temporal behaviour is heavily influenced by environmental conditions. The seasonal distributions of *Mustelus henlei* and *Triakis semifasciata* are influenced by salinity and temperature (Hopkins and Cech, 2003). Female *T. semifasciata* aggregate in large numbers in shallow environments to augment metabolic and physiological functions such as digestion, growth and reproduction (Hight and Lowe, 2007). Similarly, juvenile *M. californicus* were abundant inshore in spring and summer and became less abundant there in winter (Espinoza *et al*., 2011). Shark abundance inshore increased with water temperatures between 20 and 22˚C (Espinoza *et al*., 2011).

The habitat choice of *M. schmitti* was similarly affected by temperature and salinity but the effects varied with ontogeny (Cortés *et al.*, 2011). Juvenile *M. schmiti* prefer shallower warmer habitats with high food availability. Their behaviour was not affected by the presence of predators. On the other hand, larger *M. schmitti* occur in deeper coastal waters when not engaging in breeding activities. During breeding season, they move inshore where they sexually segregate (Cortés *et al*., 2011). Juvenile *M. antarcticus* occur in high abundances in coastal regions over summer (Barnett *et al.*, 2010). *M. henlei* use the incoming tide to access previously inaccessible foraging areas, once the tide turns they move with the tide towards the outer bay (Campos *et al*., 2009). Similarly, *T. semifasciata* used tide to access new foraging grounds (Ackerman *et al*., 2000). Movement rates of *M. henlei* increased at night

(Campos *et al*., 2009), similarly to what was observed in *T. semifasciata* (Ackerman *et al*., 2000). These studies show that the habitat choices of other triakids are heavily affected by temperature and tide. Therefore, it is expected that these environmental conditions should significantly affect the spatio-temporal behaviour of *M. mustelus* in Langebaan Lagoon.

The relationship between the distribution of species and their environment have been investigated with increasingly sophisticated statistical methods over the last decade (Leathwick *et al*.,2006). Earlier techniques such as generalized linear models (McCullagh and Nelder, 1995) were limited in their ability to incorporate non-linear relationships between movement of a species and conditions.

This chapter investigates the movement and area preference of *M. mustelus* in relation to exogenous factors at various spatial and temporal scales. Temperature and tidal profiles, measured at seabed-moored stations throughout Langebaan Lagoon area are used to describe environmental fluctuations within the shark habitat. Short-term, fine-scale movements and station keeping behaviour of sharks within the lagoon are then investigated in relation to change in tidal gradient, diel cycle, moon phase and temperature and temperature gradients. Finally, thermal preference of *M. mustelus* in Langebaan Lagoon is estimated by comparing ambient temperature readings for each shark with the temperature regime throughout the area.

METHODS AND MATERIALS

Study area

The Saldanha embayment consists of the Saldanha Bay basin, and the Langebaan Lagoon (Figure 4.1). Thermal characteristics of the system are influenced by its topography, back

radiation, convection, humidity and solar radiation (Shannon and Stander, 1977). The embayment has a strong tidal system largely unaffected by wind, with a tidal flow in the range of 10 cm s^{-1} to 20cm.s^{-1} (Shannon and Stander, 1977). Due to strong tidal movements, waters within the lagoon mix throughout the year.

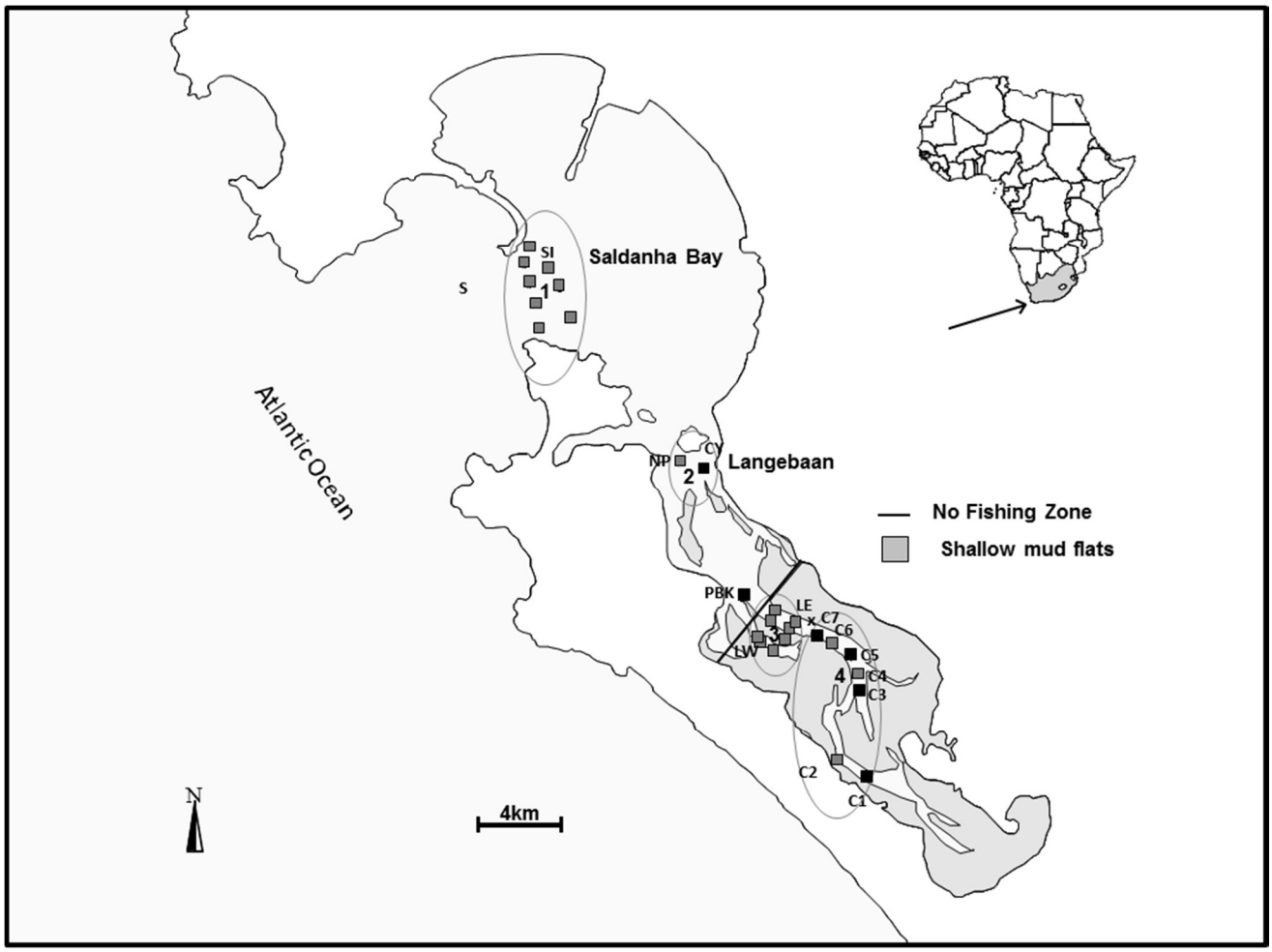


Figure 4.1. Saldanha Bay on the west coast of South Africa and its southern extension, the Langebaan Lagoon, which includes the area closed to fishing. Small grey squares denote individual receiver positions within the four receiver areas (1-4, indicated by grey circles). All individual positions are marked except for the double line of receivers at the closed area boundary (LE and LW) and the double line of receivers at the bay entrance (SI and S). Receiver positions with TDL installations are indicated by a black square. The grey shaded area within the closed area boundary represents sandbanks shallower than 2 m. The approximate catch and release location is denoted by x.

Study design

Telemetry

A total of 28 acoustic receivers (VR2, Vemco Ltd. Halifax) were moored at strategic positions throughout the bay in 2005 (Kerwath *et al*., 2009) (Fig. 4.1). Twenty-four sharks, 12 females and 12 males (length range 810- 1470 mm TL) were captured by rod and line between 8th November and 10th November 2006 with baited hooks and released with transmitters in the closed area. Sharks were anaesthetised by immersion in a seawater solution of phenoxyethanol (0.6ml^{-1}). Individually coded transmitters (VEMCO Ltd, Halifax, model V9-2L-R256, 6 KHz, random pulse rate 20-60s) were implanted into the pleuroperitoneal cavity via a 1-2 cm incision in the abdominal wall, according to methods described by Finstad *et al*., (2005). Sharks were released within the main channel inside the closed area of the Langebaan Lagoon Marine Protected Area as located in Figure 4.1. As sharks passed through the detection range of a receiver, time and tag identification number were recorded.

Environmental data collection

Two types of temperature and depth transmitters, hereafter referred to as TDL (manufactured by VEMCO, (a) model V9T measuring temperature for a maximum period of 405 days and (b) model V13TP measuring temperature and pressure for a maximum period of 779 days), were moored on the seafloor at different locations in and outside Langebaan Lagoon. V9T record temperature and V13TP record temperature and pressure (hereafter referred to as tidal elevation). Both types recorded data every 20 minutes. Between the 19th March and the 8th July 2007 V9T TDL were installed at C1, C3, C7 and the yacht club (CY) (n=4) (Figure 4.1). Between 7 December 2007 and 25 February 2008 V13TP TDL were installed at C1, C3, C5,

LW5 and PBK (n=5) (Figure 4.1). Periods when TDL data were available are summarized in Table 4.1.

Data Analysis

Seasonal fluctuations in environmental data

TDL data from 2007 were used for the description of environmental conditions (Chapter 3). The first and the last day of TDL data were removed from the analysis to avoid inclusion of records collected before and after the instrument was deployed. Data during two periods, representing winter (1st May – 7th July 2007) and summer (7th December – 24th February 2008), were examined for seasonal fluctuations in temperature. The dataset for winter included a total of 4896 records with temperature. The dataset for summer included a total of 5760 records with temperature and water pressure, a measure of tidal elevation at each TDL position (Figure 4.2).

Tidal lag was estimated by calculating the absolute difference in time between successive high tide events at TDL positions C1 and LW. Due to the large amounts of data, temperature was only plotted for the first month of data in the summer and winter periods. Wilcoxon signed rank tests were used to test if temperatures at the northernmost (LW4) and southern-most (C1) receiver were statistically different, for both the entire summer and winter period, respectively. Similarly, a Wilcoxon signed rank test was used to test if relative tidal elevation (m) at the northernmost (LW4) and southernmost (C1) positions differed.

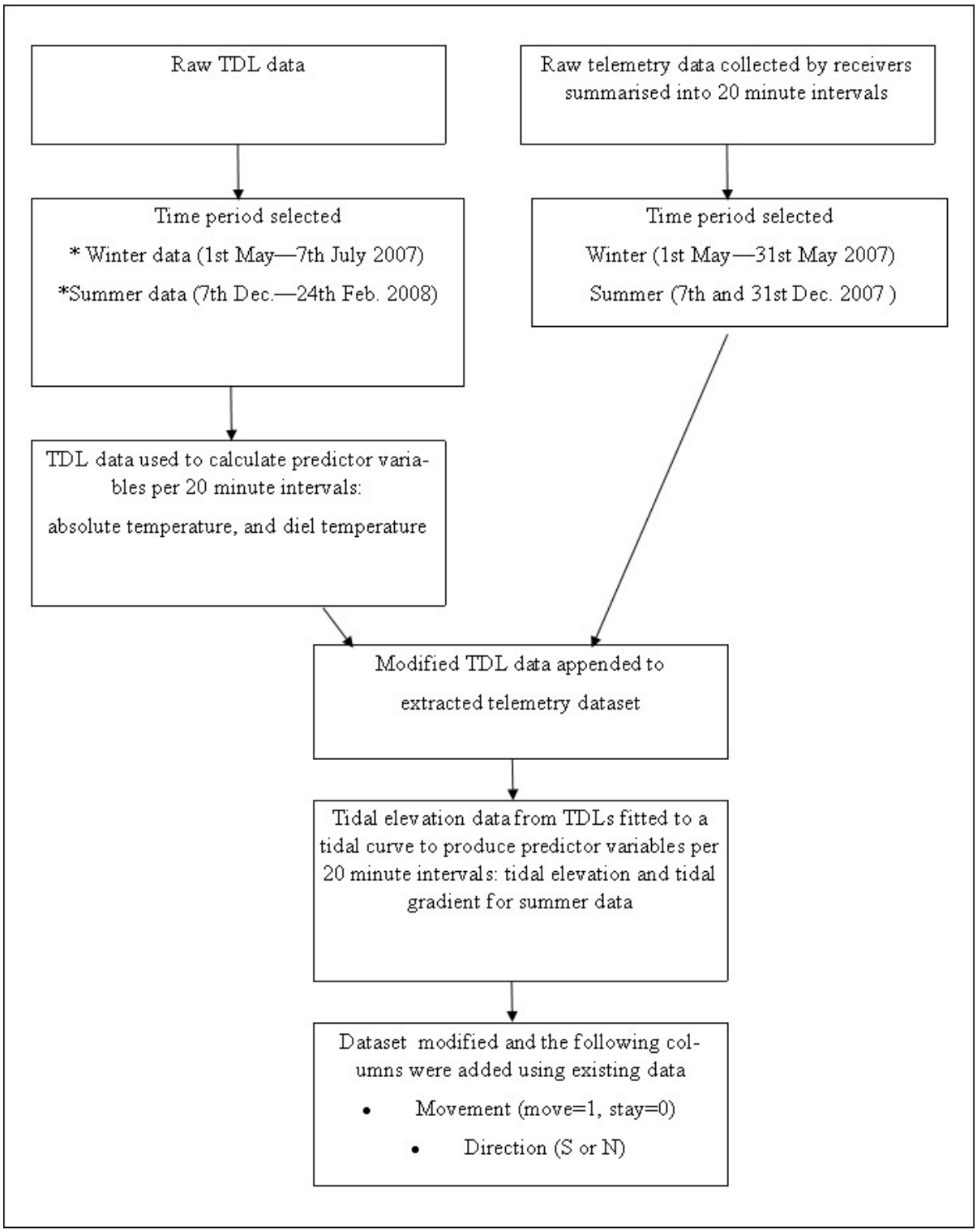


Figure 4.2. Data extraction and manipulation process

Temperature and tidal elevation data over a neap tide period (16th to 18th December 2007) and a spring tide period (9th to 11th December 2007) were extracted from raw data and described. Students t-tests were used to investigate the hypothesis that there was no difference between tidal elevation among for neap and spring tide periods.

Table 4.1. TDL data available per position.

Position	Temperature data	Pressure data
C1	2007/03/19-2007/07/08	2007/12/06-2008/02/25
	2007/12/06-2008/11/12	
C3	2007/03/19-2007/07/08	2007/12/06-2008/02/25
	2007/12/06-2008/06/16	
C5	2007/12/06-2008/06/16	2007/12/06-2008/02/25
C7	2007/03/19-2007/07/08	2008/02/28-2008/11/13
	2008/02/28-2008/11/13	
LW4	2007/12/06-2008/11/13	2007/12/06-2008/02/25
		2008/07/23-2008/11/13
PBK	2007/12/06-2008/02/27	-
Yacht club	2007/03/19-2007/07/08	-

Fine-scale movement in relation to abiotic conditions

Descriptive observations

The movements of sharks with >30 known positions within the first week 7th to 14th December 2007 were plotted separately to show fine-scale movements. To determine if shark movements were synchronised among individuals, the number of sharks which moved in the same direction was calculated for each 20-minute interval and for each 1 hr interval. The presence of male and female sharks at the northern-most and southern-most positions at night

and day was tested using x^2 tests. Similarly, the prevalence of immature and mature sharks at the northern-most and southern-most positions at night and day was tested using x^2 tests.

Presence of M. mustelus in relation to temperature

Raw TDL data were extracted for the summer (7th December – 31st December 2007) and winter (1st May – 31st May 2007) periods. Telemetry data in 20-minute intervals was extracted for from the summer and winter periods and appended to the TDL data. Figure 4.2 explains the data manipulation process prior to analysis of individual shark temperature preferences of *M. mustelus*.

This dataset represents a sequential set of positions at 20-minute intervals for each of the 15 sharks from Chapter 3, and a sequential set of movements relative to the preceding time interval. The temperature at each position during one time interval was appended to the dataset. A total of 1800 records for the period between 7th and 31st December 2007 and 2233 records for the period between 1st May and 31st May 2007 were available for each of the 15 sharks. For analyses of individual temperature preferences, all time intervals with no known positions were removed. This consisted of 2381 records with known positions in summer and 2176 records with known positions in winter (Table 4.2).

A frequency distribution of each shark's occurrence across the temperature spectrum was calculated by dividing the number of detections of each shark in each 1 degree temperature interval by the total number of detections of that shark. The concurrent ambient temperature distribution was also plotted for comparison. The difference between the average temperatures in which sharks spent their time and the available average temperatures was tested using a student's t-test for each shark individually as data was normally distributed and

test results are provided on the above-mentioned graphs. The differences between the average temperatures in which female and male sharks spent their time was tested with a Kruskal-Wallis test. Similarly, the difference in average temperatures in which immature and mature sharks spent their time was tested with a Kruskal-Wallis test.

To determine if sharks exhibited affinity for or avoidance of specific temperature regimes within the LMPA (Heupel and Simpfendorfer 2008), the temperature at which tagged sharks occurred were compared to those available in the closed area using Chesson's electivity index (Chesson, 1978):

$$electivity_i = \left(\frac{r_i}{p_i}\right) / \sum\left(\frac{r_i}{p_i}\right) \quad [1]$$

Where r_i is the proportion of the time that the sharks spent at temperature category i, and p_i is the proportion of the closed area at temperature category i.

.Chesson's α is calculated in the following way:

$$\alpha = \left({}^{1}/_{number\ of\ categories}\right) \quad [2]$$

The electivity profile is then standardized by Chesson's α to centre the index on zero.

$$electivity\ deviance_i = (electivity_i - \alpha)/\alpha \quad [3]$$

Electivity deviance values above 0 indicate affinity, whereas values below indicate avoidance.

Table 4.2 The number of position recordings per shark by season

Shark	Summer	Winter
a	151	109
b	170	7
c	8	31
d	64	3
e	74	215
f	132	220
g	176	78
h	233	208
i	306	288
j	279	148
k	192	
l	100	
m	57	133
n	319	574
o	120	161

Fine scale spatio-temporal behaviour in relation to environmental conditions

Telemetry data from 7th to 31st December were extracted to match the period when TDL data were available. As the TDL were placed within the closed area channels close together (Distance between C1 and LW5 = 4.33 km), it was possible to analyse fine scale movement behaviour in relation to environmental conditions.

Telemetry data were standardised into a sequential set of data using the procedure described in Chapter 3 with the difference that the data were parsed into 20-minute intervals rather than

one-hour intervals. This was done to align that telemetry data to the environmental data that was logged at 20-minute intervals. The resulting standardised data (as in Chapter 3) consisted of a sequential set of positions per shark per 20-minute interval. If the shark was not detected in a 20-minute interval, no position could be assigned to that interval. Shark movement (*0* = no movement; *1* =movement from one position to another) and direction of movement (*S*; *N*) were categorized in the following manner: If a shark was recorded at a position in a given 20-minute time-interval that was identical to the position in the previous 20-minute interval it was assigned a value of "0". If a shark was recorded at a different position it was assigned as 1". Movement between positions towards the top of the lagoon were classified as "*S*", and towards Saldanha Bay as "*N*". After removing the time intervals where the position of individual sharks was unknown, a total of 2448 shark position records remained. Because movement and directional estimates required at least two consecutive position records, only 1043 records with movement and directional data were available. Of these, 809 were "no movement" records, 67 were "*S*" and 107 were "*N*". *Diel pattern,* described as one of four categories (*dawn, day, dusk, and night*) and moon phase described as one of eight categories (*full moon, waning gibbous, first quarter, waning crescent, new moon, waxing crescent, third quarter and waxing gibbous*) were appended to the telemetry data from 7-31st December 2007 (Figure 4.2).

Raw TDL data between the period 7th and 31st December 2007 were also extracted. Through the use of this raw data, the following predictor variables were appended to the extracted dataset: *Absolute Temperature* (*abs. T*), *Delta Temperature* (*dT*) and *Tidal elevation* and *Flow* (details below). These variables were calculated in the following way: For each 20-min interval, absolute temperature was assigned to each receiver position. If a receiver position

did not have a TDL, the temperature was approximated by that of the closest instrument (Table 4.3).

The resulting data consisted of a sequential set of positions and *absolute temperature* per shark per 20-minute interval. *Delta temperature* was calculated as the difference in temperature between *absolute temperature* and the temperature at the same position 20 minutes earlier to determine if the water at the position was warming (+) or cooling (-).

Tidal elevation and *gradient,* represented by the relative tidal height and the relative change thereof, was calculated by the tidal model in the following way: Raw data from the TDLs included depth data in m. Tidal elevation was calculated as the difference in depth between the depth at a particular position and the depth at that position 20 minutes earlier from the raw TDL data between 7th December 2007 and 31st December 2007. These data were used to model the dynamics of tidal elevation and the gradients across the receiver array. A sine curve was fitted to tidal elevation data at each TDL station for each 12-hour cycle. The tidal height was modelled as a modified sine curve, as follows:

$h\,(t) = \mathrm{A} \sin \mathrm{C}\,(t - \mathrm{S}) + \mathrm{L}$ [4]

where *h (t)* is tidal height at time t, *A* is the amplitude in m, *C* is the number of cycles in the curve, *S* represents the time offset), and *L* represents the height offset. Parameter estimates of *A*, *C*, *S* and *L* for each receiver were obtained by minimising the sum of squares of the difference between pressure values and *h (t)*

$$ss = \sum_{t=1}^{n} (t_i - \hat{t}_i)^2 \quad [5]$$

where t_i and $\hat{t}_i$ are the observed and model predicted tidal height (m.) at time interval *i* and *n* represents the number of time intervals. Tidal flow was approximated with a cosine function such that the strongest flow corresponded to midway between high and low tide. The model

was fitted for each tidal cycle (12h), and the estimates, which denote relative *tidal elevation* and *relative tidal gradient* were appended to corresponding 20-minute intervals in the telemetry dataset from 7th to 31st December 2007.

For illustrative purposes, an extract and example of data with telemetry data and environmental variables used for the analysis of fine-scale spatio-temporal behaviour is depicted in Table 4.4 to show the structure and format of the data.

Table 4.3 TDLs used to represent areas within the closed area and SB

TDL site	Area represented
C1	C1, C2
C3	C3, C4
C5	C5, C6, C7
LW5	LE, LW, PBK, NP, SI, S

Table 4.4 An example of the final appended dataset used for analysis of fine-scale spatio-temporal behaviour. *Shark id* denotes the individual telemetered shark. Receiver denotes the position at which the shark was recorded during that time interval. *Movement* in the preceding time interval is recorded as a binary variable. *Direction* shows if the movement in preceding time interval was toward the closed area (*S*) or towards SB (*N*). *Diel* represents the diel period (*night*, *dawn*, *day* and *dusk*), and *moon* represents the moon phase during time interval (*full moon, waning gibbous, first quarter, waning crescent, new moon, waxing crescent, third quarter and waxing gibbous*). *abs. T* represents the *absolute temperature* experienced at the TDL closest to the position where the telemetered shark was recorded. *dT* represents the change in temperature in the time interval. *Tide* denotes the tidal phase (low tide scores -1, high tide +1).

Date time	Shark id	Receiver	Movement	Direction	Diel	Moon	Abs.T	dT	Tide	Flow
2007/12/07 00:00	d	C5	0	Na	Night	Wanc	18.6	0	-0.004	1.00
2007/12/07 00:00	e	LW	1	Na	Night	Wanc	17.8	0	-0.007	1.00
2007/12/07 00:40	a	LW	0	Na	Night	Wanc	17.7	-0.1	0.73	0.67
2007/12/07 01:00	g	LE	1	S	Night	Wanc	17.5	-0.3	0.95	0.32
2007/12/07 01:20	h	LE	0	Na	Night	Wanc	17.1	-0.6	1.00	0.09

Effect of abiotic variables on movement

A number of generalised additive and generalised additive mixed models were fitted to the binary response data (i.e. 1 or 0 for *Movement* and *Fish Direction)* using the 'mgcv' package (Wood 2006) in 'R' (R development Core Team 2008; http:///CRAN.R-project.org/) to determine if they were influenced by predictor variables. Two different responses were investigated; *Movement* (a movement away from a known position constitutes a movement; 1 and 0) and *Fish direction* (movement between two known positions during consecutive time intervals with the following directions; *S* (towards the closed area (0)), *N* (towards the Saldanha Bay (1)). For each movement criteria, the following predictor variables were investigated (Table 4.5): *Absolute Temperature* (*abs. T*), *delta Temperature* (*dT*), *diel pattern* (*Dawn, dusk, day and night* as in Chapter 2), *moon phase* (*full moon, waning gibbous, first quarter, waning crescent, new moon, waxing crescent, first quarter* and *waxing gibbous*) and *tide* (as described above). To predict the influence of individual predictor variables on the probability of movement, a reference set of standardized conditions was constructed by setting *abs. T* and *dT* to the median. These predictions were plotted.

Table 4.5 Description and nature of predictor variables analysed in this study

Predictor variable	Categorical or continuous	No of categories	Spline (y/n)	Cyclical data (y/n)
Absolute temperature (abs. T)	Continuous	na	Y	N
Delta temperature (dT)	Continuous	na	Y	Y
Diel pattern	Categorical	4	N	N
Moon phase	Categorical	8	N	N
Tide	Continuous	na	N	Y
Flow	Continuous	na	N	Y

The general additive model is given by:

$$logit(\hat{p}) = \beta_0 + f_1(X_i) + f_2(X_i) + \cdots + \varepsilon_i \quad \text{where } \varepsilon_i \sim n(0, \sigma^2) \qquad [6]$$

where $\hat{p}$ represents the probability of a shark moving between different time intervals or the probability of a shark moving in a particular direction. X_i are covariates, β_0 represents regression coefficients, *n* represents the number of applicable predictor variables, *i* represents the observation at interval *i*, f_1 and f_2 denotes the smoothing functions realized by thin plate spline regression functions and ε_i is the model residual or error which is distributed between 0 and σ^2. σ^2 represents the variance.

The probability of a shark moving between different time intervals or the probability of a shark moving in a particular direction could be expressed as:

$$logit(p) = \beta_0 + f_1(abs.T) + \text{diel} + f_2(dT) + f_3(moon) + tide + flow + \alpha_i \qquad [7]$$

where α_i denotes the random effect of the individual sharks.

The most parsimonious models were selected by evaluating the optimal combination of predictor variables using Akaike's Information Criterion and Bayesian Information Criterion (Zuur et al 2009). Sequential F-tests were used to determine the predictor variables that

contributed significantly ($p < 0.05$) to the deviance explained. Finally, the probabilities of a shark moving at different time intervals and the probability of a shark moving in a particular direction were predicted individually for all significant environmental variables while all other factors were kept constant at mean or median values.

RESULTS

General abiotic conditions in the closed area

On average the water was warmer at the southern-most portion of the lagoon. In winter, the average temperature gradient along the lagoon was 1.4 ° C (Table 4.6). Temperature variations in the period 1 May to 7 July 2007 were more extreme at the southern-most part of the Lagoon than near the closed area boundary (Table 4.6). Overall, the temperature in the summer period from 7 December to 24th February 2008 was 6.8 ° C warmer than the winter period of 2007 (Tables 4.6- 4.7). In summer, the average temperature gradient along the lagoon was 2.5° C, being warmer at the southern-most end (Table 4.7). In the summer, and in contrast to winter, the temperature variation near the closed area boundary was more extreme than at the southern-most end (Tables 4.6-4.7). Another important contrast between the two periods was the location of the minimum temperature in the system. In winter, the lowest temperature was experienced at the southern-most position within the closed area (10.7 ˚C), however, in summer the lowest temperate was experienced outside the closed area (12.7 ˚C).

High resolution extracts of the temperature series for winter (1st – 31st May 2007) and summer (7th – 31st Dec. 2008) are displayed in Figure 4.3. Temperature variations of both periods to a large extent are driven by tidal exchange. Temperature fluctuations are stronger in summer (up to 7.0 °C tidally induced) than winter (up to 2.5 °C tidally induced) at C1. At

LW4, the tidally induced variability is less than half of the equivalent variability at C1 in summer. In winter, the tidal induced variability is similar between the two sites. This pattern changes in winter (around the beginning of May) when the difference between the areas disappears and the variation in absolute temperature decreases. This corresponds to the periods when two sharks left Saldanha Bay (Figure 4.3). In winter, temperature at the southern-most boundary ranges between 13.2 and 19.6 ° C in the day (average=16.3° C) and 13.0 and 19.1 ° C at night (average = 16.4° C). Temperature at the closed area boundary ranges between 13.5 and 17.5° C in the day (average =15.3° C) and 13.6 and 17.4° C at night (average = 15.4° C). In summer, temperature at the southern-most boundary ranges between 18.8 and 25.6 ° C in the day (average = 22.5 ° C) and 18.6 and 26.1° C at night (average = 22.6° C). Temperature at the closed area boundary ranges between 16.0 and 24.5 ° C in the day (average = 19.8° C) and 14.9 and 24.7 ° C at night (average = 20.4° C)

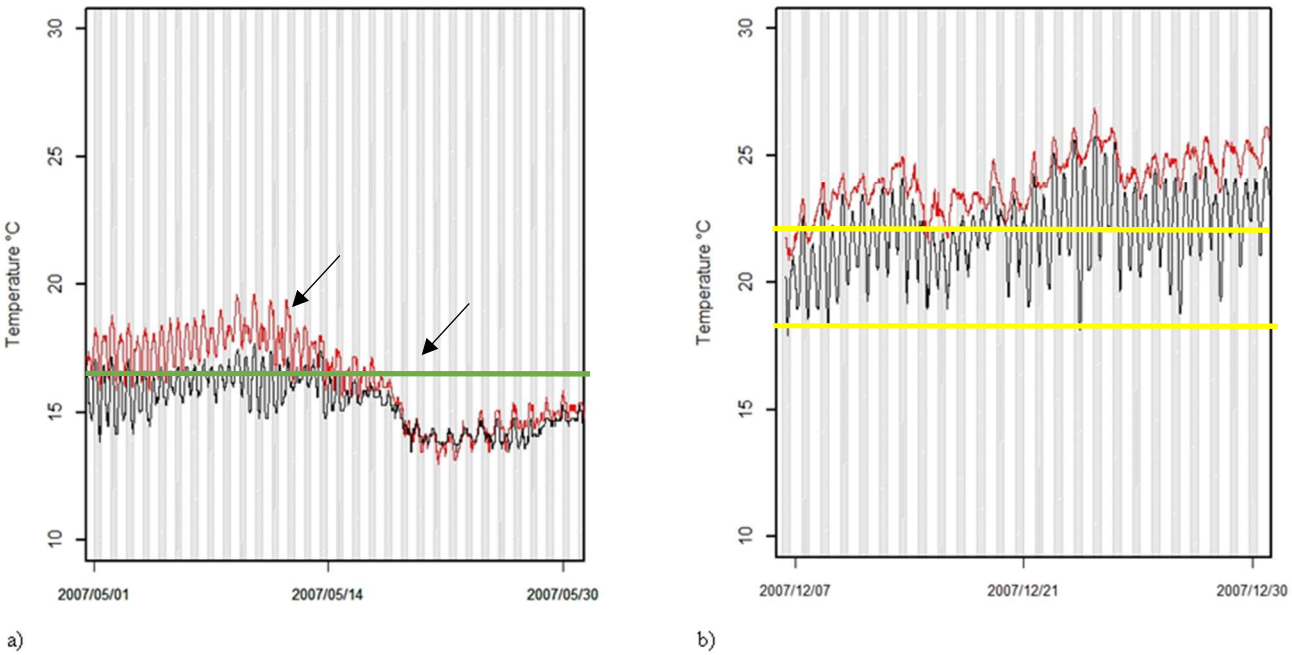


Figure 4.3. Temperature (˚C) data from TDLs placed at the northernmost position (LW4) in black and southern-most position (C1) red inside the closed area between the a) 1st and 31st May 2007, representing a month in winter and b) 7 December and 31 December 2007 in the closed area and Saldanha Bay surrounds representing summer conditions. Grey bars represent night time periods. Yellow lines in summer indicates thermal preferences of 18- 22 ˚C for *M. mustelus* originating from GAMM results while the green line in winter indicates the mean temperature in which *M. mustelus* spent their time in winter. Arrows represents the period where sharks *j* (19th May 2007 for 139 days) and *n* (12th May 2007 for 157 days) left the Saldanha embayment.

Table 4.6 Temperature recorded at 20-minute intervals by the four TDLs showing the mean temperature, minimum temperature, maximum temperature and standard deviation between 1 May 2007 and 7 July 2007 in the closed area representing winter periods. The last row represents mean temperature, minimum temperature, maximum temperature and standard deviation across all receivers with TDLs.

Position	Mean temperature (°C)	Minimum temperature (°C)	Maximum temperature (°C)	Standard deviation (°C)
C1	15.0	10.7	19.6	1.8
C3	14.8	11.2	19.6	1.8
C7	14.8	11.3	19.0	1.5
LW4	14.6	12.1	17.7	1.1
All	14.8	10.7	19.6	1.6

Table 4.7 Temperature recorded at 20-minute intervals by the four TDLs summarised as the mean temperature, minimum temperature, maximum temperature and standard deviation. The data were collected between 7 December 2007 and 24 February 2008 in the closed area and Saldanha Bay surrounds representing summer periods. The last row represents mean temperature, minimum temperature, maximum temperature and standard deviation across all receivers with TDLs.

Position	Mean temperature (°C)	Minimum temperature (°C)	Maximum temperature (°C)	Standard deviation (°C)
C1	21.8	18.3	26.2	1.4
C3	20.9	15.2	25.9	1.8
C5	20.5	14.6	25.6	1.8
LW4	19.4	12.7	24.7	2.1
All	20.6	12.7	26.2	2.0

The overall average tidal lag was 31 minutes (range 16- 96 minutes, SD = 26) between positions LW4 and C1. Tidal amplitude ranged between 0.8 and 1.6 m (Table. 4.8), depending on the location. A larger variation was experienced at position LW4 than all other positions at 1.6 m followed by C3 at 1 m and both C5 and C1 at 0.8 m. Due to missing tidal height data in winter, seasonal differences could not be determined**.**

Table 4.8 The minimum and maximum tidal elevation and standard deviation recorded at moorings C1 to LW4 during a full spring tidal cycle in the period 7th December to 31st December 2007.

Position	Minimum tidal elevation (m)	Maximum tidal elevation (m)
C1	-0.4	0.4
C3	-0.5	0.5
C5	-0.4	0.4
LW4	-0.8	0.8
All	-0.8	0.8

Fine scale movement in relation to abiotic conditions in the closed area

Fine scale movement

Fine scale individual movement trajectories are shown for the first week of data in the summer period (7th to 14th December 2007). These data show movement from the eight sharks with the most data (Figure 4.4). In general, individual sharks show a back and forth movement between positions representing their southern-most and northern-most limits. The majority of movements (95%) are between positions C3 and LW (within the closed area boundary), however, on occasion sharks do extend their movements outside the boundary of the closed area. There was a significant difference in the use of the northern-most and southern-most positions during different diel periods, with immature sharks avoiding the southern-most positions at night (n=15, x^2 test, $x^2 = 129.4$, p-value **< 0.05**) (Figure 4.4 example shark *a*, *b* and *h*). Mature sharks do not appear to restrict their movements southwards during day time (*i*, *j*, *k*, and *o*) (Figure 4.4). There was also a significant

difference in area use during different diel periods for sex, males in general avoided the southern-most positions at night (n=15, x^2 test, $x^2 = 58.03$, p-value **< 0.05**).

Very little synchronicity in the direction of movement among sharks was recorded within 20-minute intervals or within 1 hour intervals (Table 4.9). Rarely did more than one shark move in the same direction during the same 20-minute interval. In less than 10% of all 20-minute time intervals did two or more sharks (out of a maximum of 15) move in the same direction. At no point during this observation period did more than 3 sharks move at the same time between 20-minute intervals. Synchronicity was greater in the one hour interval. Approximately a quarter of one hour intervals had two or more sharks moving in the same direction (Table 4.9).

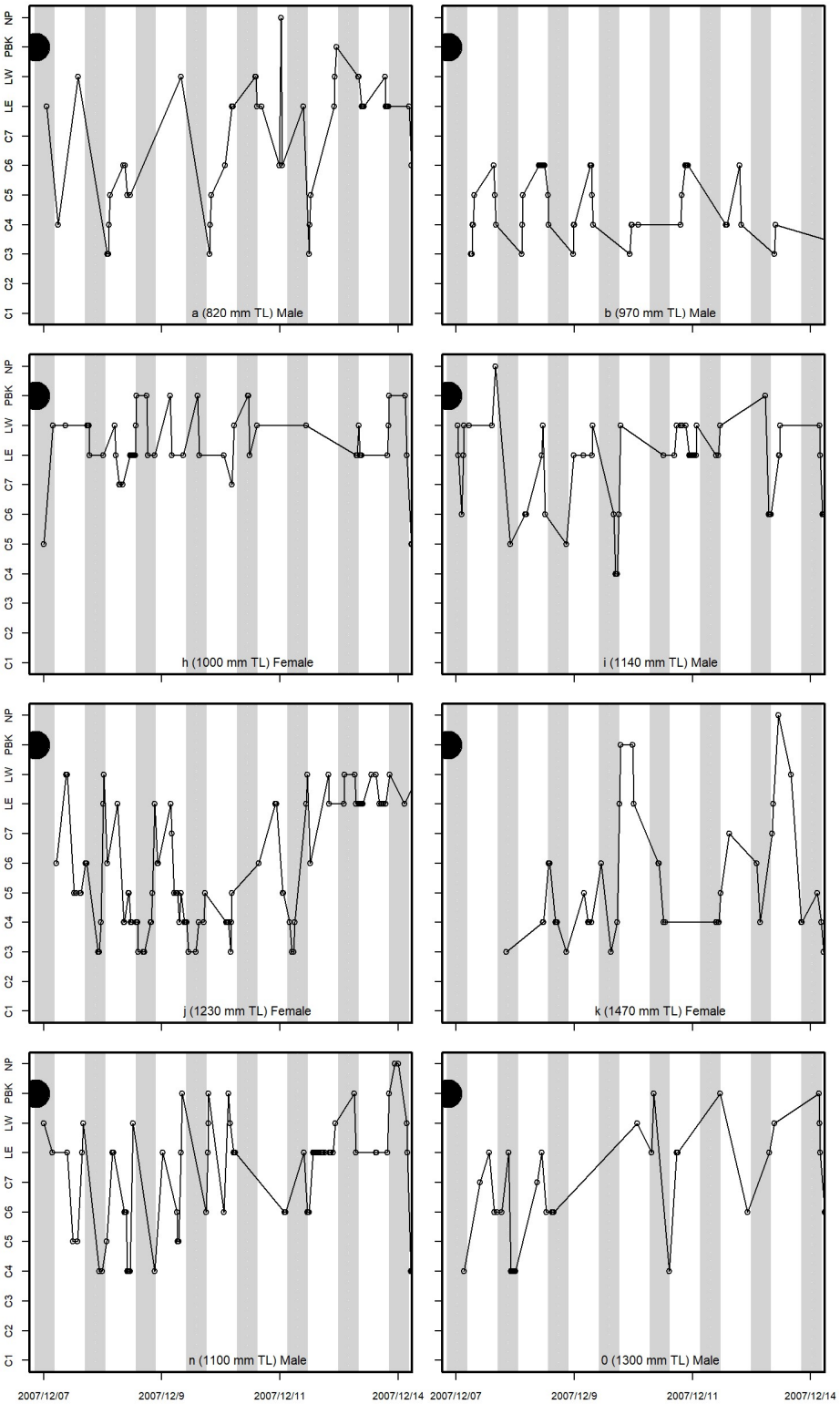


Figure 4.4. Fine scale movement of individual *M. mustelus* (*a*, *b*, *h*, *i, j, k, n, o*) within the closed area and surrounds between the 07th and 14th December. New moon is represented as a solid circle.

Table 4.9. The percentage of time intervals in which synchronous movements were made by varying numbers of sharks out of a total of 15 present inside the closed area during the period are listed. Lack of synchrony in shark movements occurred in 91.6 % of time intervals.

Number of sharks moving synchronously	(%) Frequency of 20-minute intervals	(%) Frequency of 1-hour intervals
2	5.1	21.6
3	3.2	0.8
4	0.0	2.4
5	0.0	0.8
6	0.0	0.0
7	0.0	0.8

Presence of M. mustelus in relation to temperature

The temperatures experienced by sharks in relation to ambient temperature in winter are shown in Figures 4.5-4.6. During winter the water temperature where sharks spent their time ranged between 13.0 and 19.1 °C (average =15.9 °C, SD = 1.2). The ambient temperature recorded by the TDLs ranged between 13.0 and 19.6 °C (average = 15.9 °C, SD = 1.5). Differences between the temperatures where sharks spent their time and ambient temperature in winter differed by up to 2.0 °C

The temperatures where the sharks spent most of their time were significantly different than the ambient temperature for eight of ten sharks observed in winter (Figs 4.5 –4.6). In winter for five (*a*, *b*, *f*, *g*, *o*) of the 10 sharks, sharks preferred temperatures significantly warmer than average ambient temperature. Three of the ten sharks *g*, *h* and *n* preferred water significantly colder than available ambient temperature. The average temperatures in which

female sharks spent their time was significantly different and warmer than males in winter (n = 10, Kruskal-Wallis test, x^2 = 12.09, DF=1, p-value < **0.05**) (Figure 4.7). The average temperatures in which immature sharks spent their time was significantly different and warmer than mature sharks in winter (n = 10, Kruskal-Wallis test, x^2 = 45.05, DF=1, p-value < **0.05**) (Figure 4.7).

The temperatures experienced by sharks in summer in relation to average temperature are shown in Figures 4.8 – 4.9. During summer the water temperature where animals spent their time ranged between 15.4 and 25.2 °C (average = 20.5 °C, SD = 1.7), while the available temperature recorded by the TDLs ranged between 14.9 and 26.1 °C (average = 21.3 °C, SD = 1.9) (Figures 4.8-4.9). Differences between the temperatures where sharks spent their time and ambient temperature in summer differed by up to 2.0 °C. The average temperatures in which sharks spent most of their time were significantly different from the available average temperatures for 13 of 14 sharks observed in summer (Figures 4.8 - 4.9). One shark did not sufficient data during this period. Sharks preferred temperatures significantly colder than available ambient temperature. The sharks preferred a slightly cooler environment that was available on average in the lagoon in summer. The average temperatures in which female sharks spent their time was significantly different warmer than males in summer (n = 14, Kruskal-Wallis test, x^2 = 30.37, DF=1, p-value < **0.05**) (Figure 4.10). The average temperatures in which immature sharks spent their time was significantly colder than mature sharks in summer (n = 14, Kruskal-Wallis test, x^2 = 5.97, DF=1, p-value = **0.01**) (Figure 4.10).

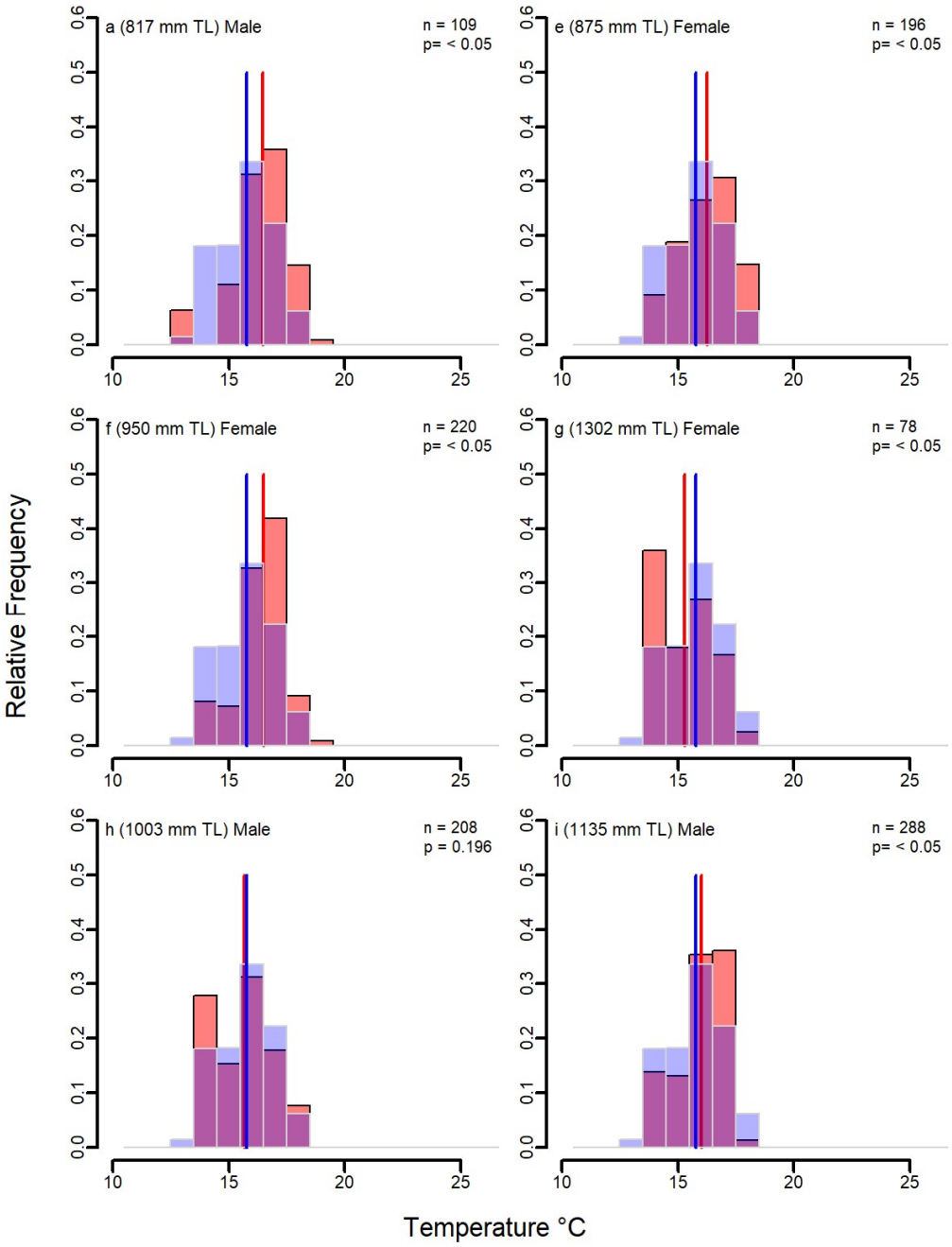


Figure 4.5. Temperature distribution (°C) experienced by six individual sharks present inside Langebaan Lagoon between the 1th and 31st of May 2007 are shown in red. Average ambient temperatures from thermographs placed at receiver locations C1, C3, C7 and CY are shown in blue. Purple areas represent the overlap between the two. P-values from Kruskall-Wallis tests are displayed. Red vertical line represents the median temperature where sharks were found, while the blue vertical line represents the median average ambient temperature. n represents the number of bins from the temperature distribution of each shark.

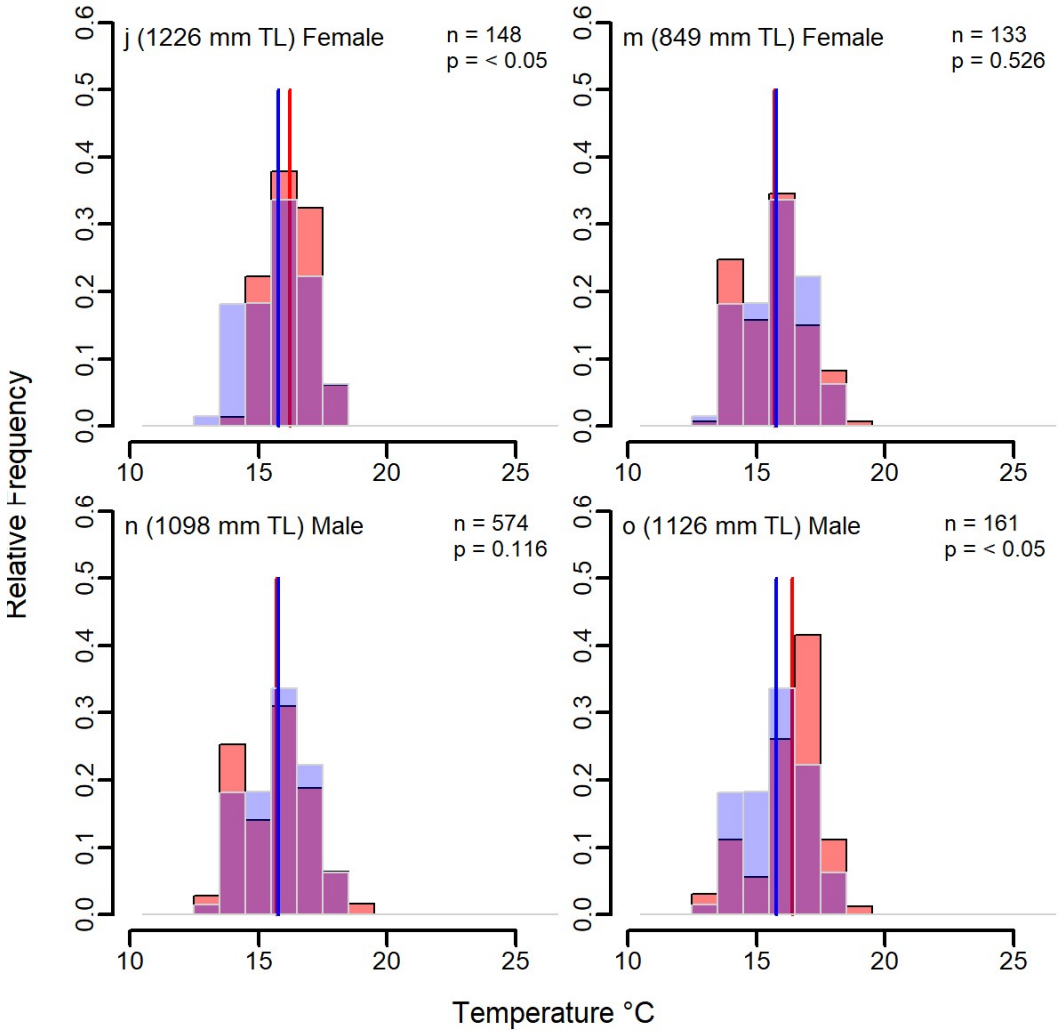


Figure 4.6. Temperature distribution (°C) experienced by four individual sharks present inside Langebaan Lagoon between the 1th and 31st of May 2007 are shown in red. Average ambient temperatures from thermographs placed at receiver locations C1, C3, C7 and CY are shown in blue. Purple areas represent the overlap between the two. P-values from Kruskall-Wallis tests are displayed. Red vertical line represents the median temperature where sharks were found, while the blue vertical line represents the median average ambient temperature. n represents the number of bins from the temperature distribution of each shark.

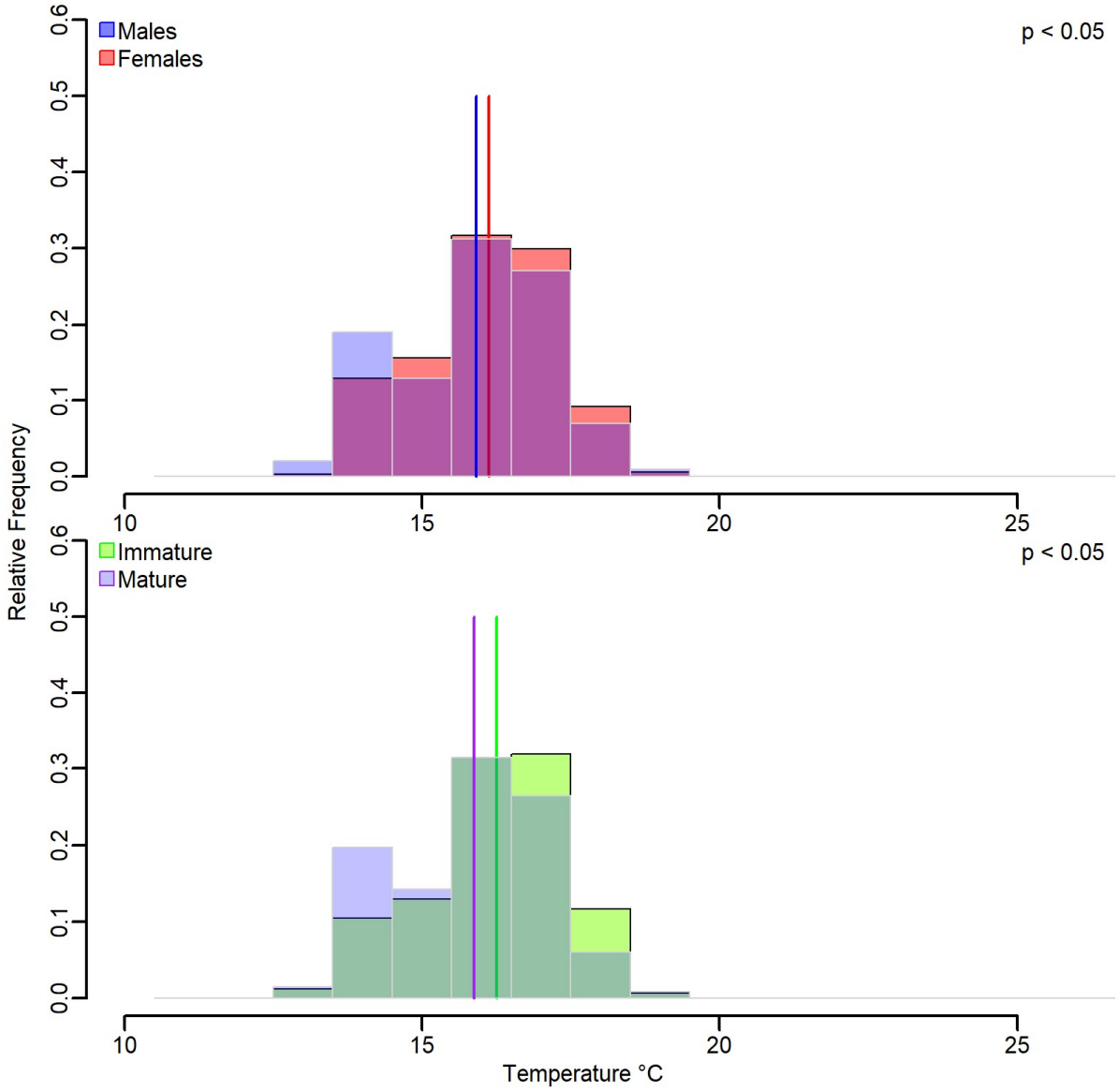


Figure 4.7 Temperature distribution (°C) experienced by each sex (red and blue bars) and maturity states (green and purple bars) for *M. mustelus* present inside Langebaan Lagoon between the 1st and 31st May 2007. Purple areas represent an overlap between temperatures where female and male sharks were found. Dark green areas represent an overlap between temperatures where immature and mature sharks were found. P-values from Kruskall-Wallis tests are displayed.

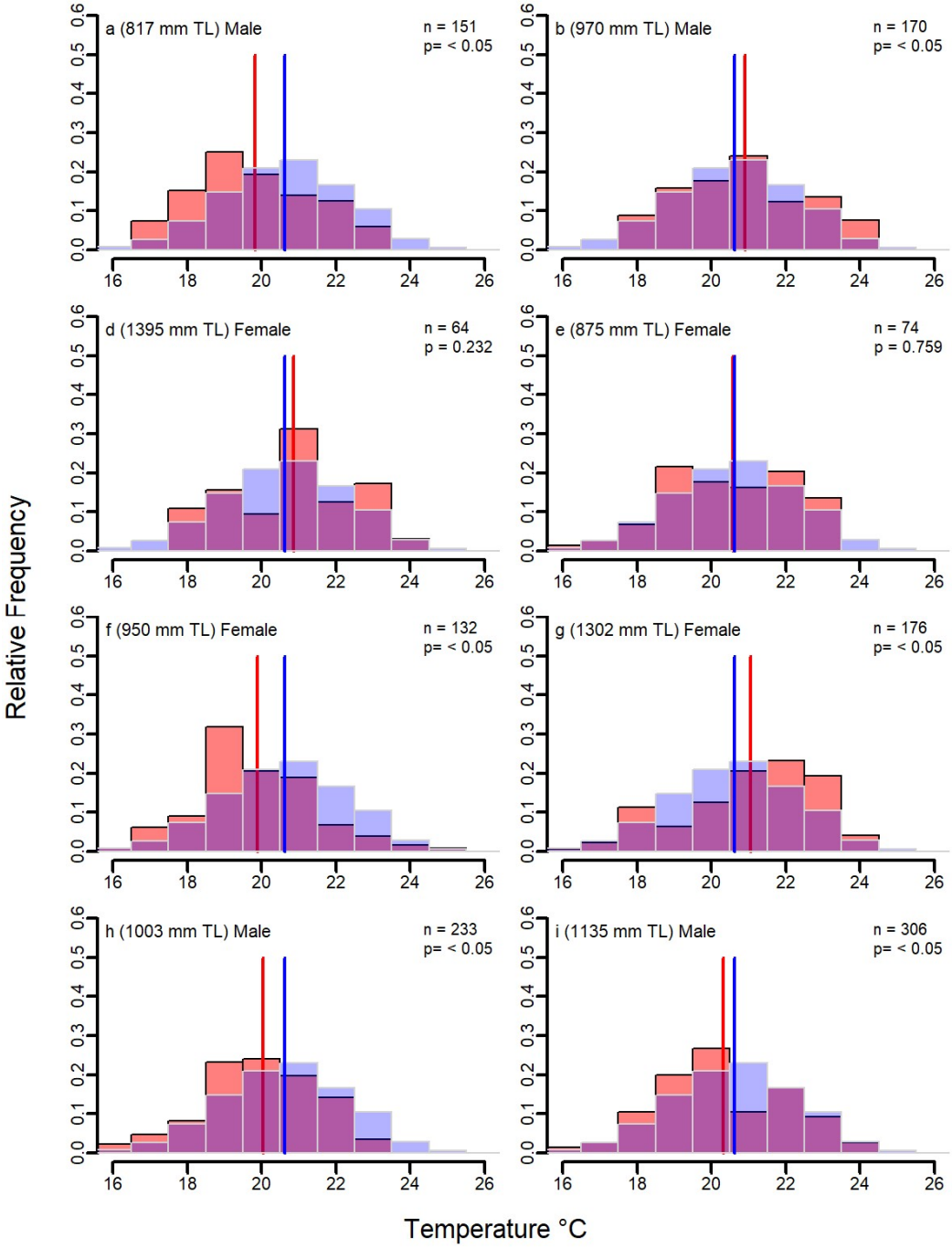


Figure 4.8. Temperature distribution (°C) experienced by eight individual sharks present inside Langebaan Lagoon between the 7th December 2006 and 31st December 2007are shown in red. Average ambient temperatures across thermographs placed at receiver locations C1, C3, C5 and LW5 are shown in blue. Purple areas represent the overlap between the two. P-values from Kruskall-Wallis tests are displayed. Red vertical line represents the median temperature where sharks were found, while the blue vertical line represents the median average ambient temperature. n Represents the number of bins from the temperature distribution of each shark.

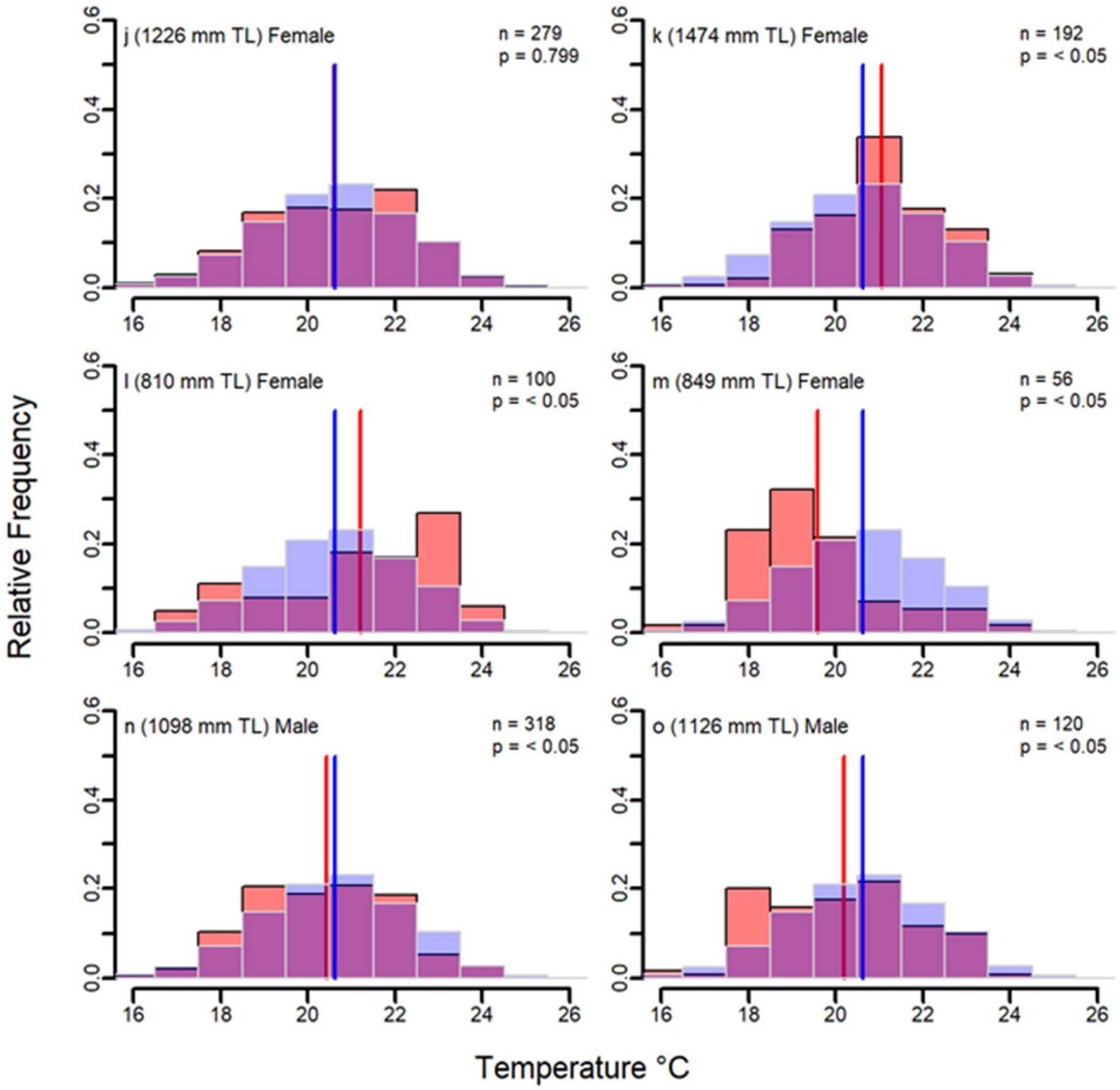


Figure 4.9. Temperature distribution (°C) experienced by six individual sharks present inside Langebaan between the 7th and 31st of December 2007 are shown in red. Average ambient temperature from thermographs placed at receiver locations C1, C3, C5 and LW5 shown in blue. Purple areas represent the overlap between the two. P-values from Kruskall-Wallis tests are displayed. Red vertical line represents the median temperature where sharks were found, while the blue vertical line represents the median average ambient temperature. n represents the number of bins from the temperature distribution of each shark

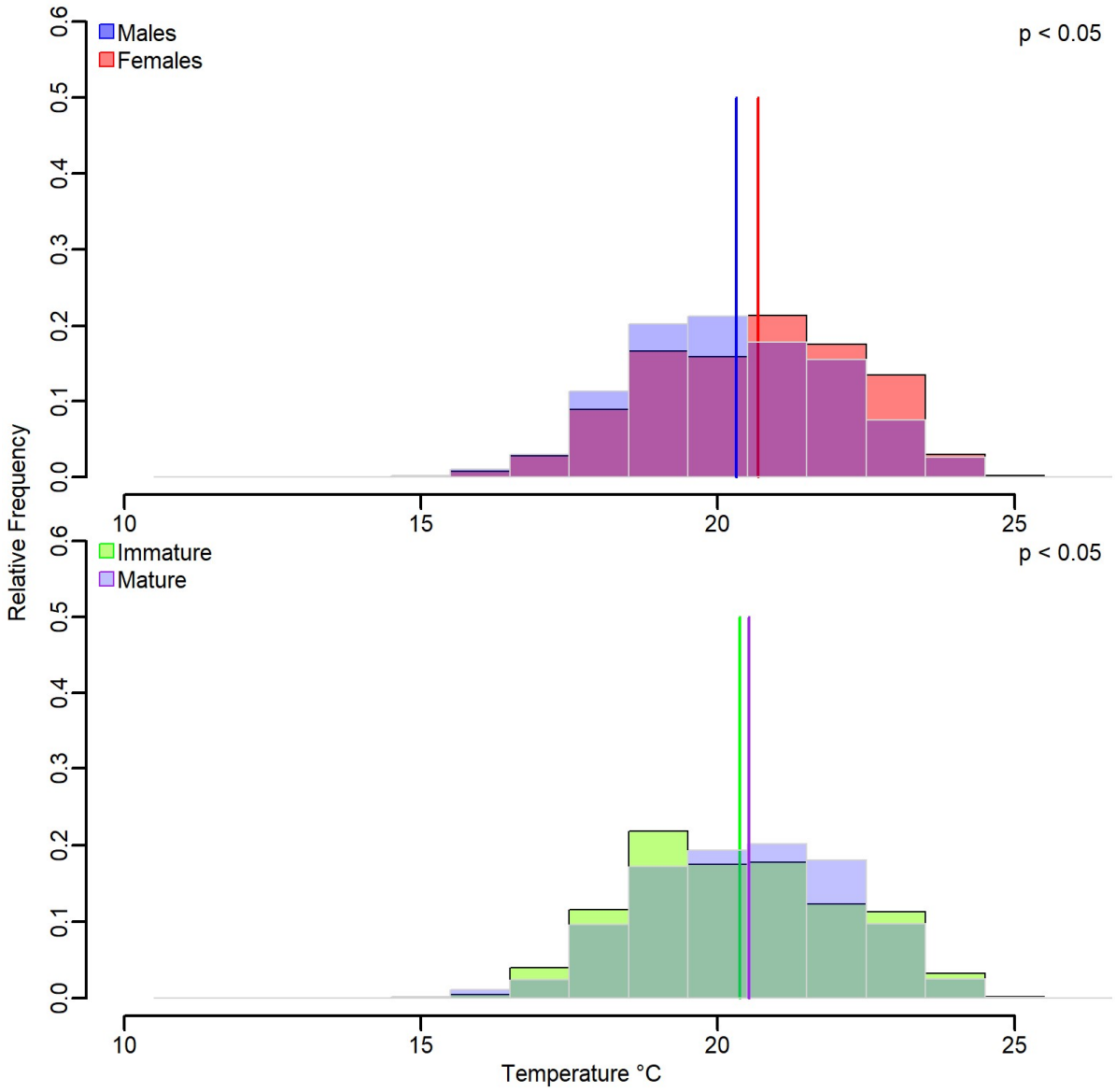


Figure 4.10. Temperature distribution (°C) experienced by each sex (red and blue bars) and maturity states (green and purple bars) for *M. mustelus* present inside Langebaan Lagoon between the 7th and 31st December 2007. Purple areas represent an overlap between temperatures where female and male sharks were found. Dark green areas represent an overlap between temperatures where immature and mature sharks were found. P-values from Kruskall-Wallis tests are displayed.

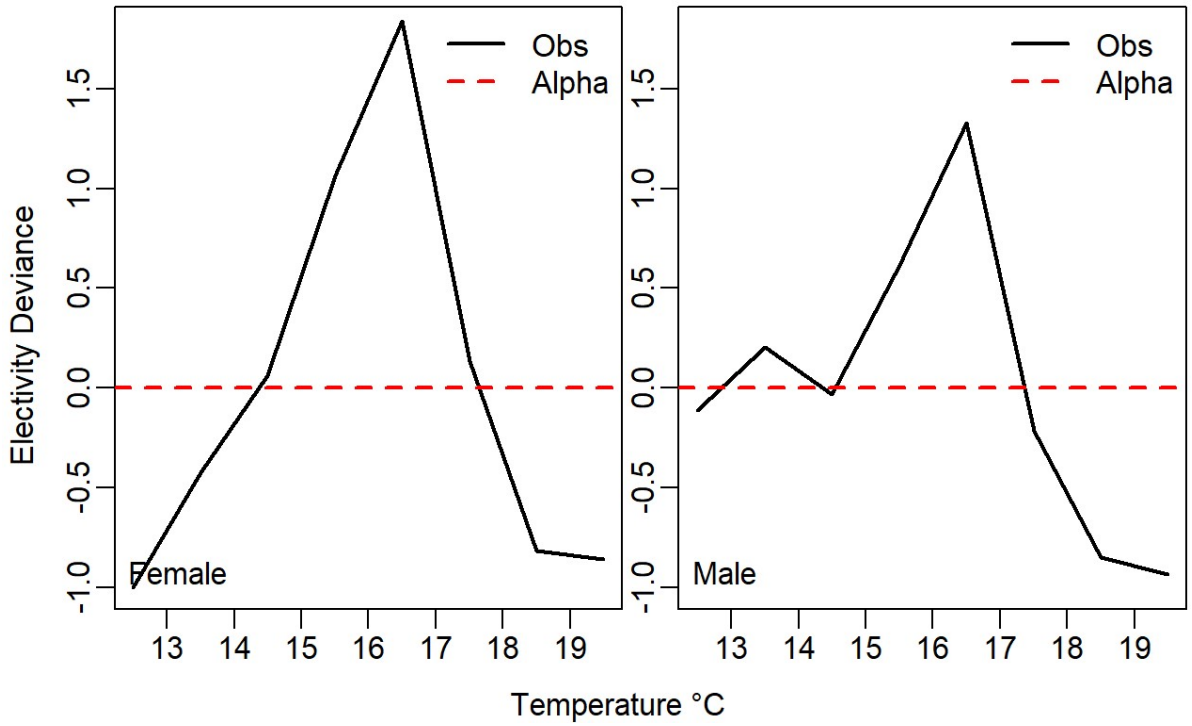


Figure 4.11. Temperature electivity analysis for *M. mustelus* in winter, showing the electivity values standardized by the value of Chesson's α (electivity deviance); values above 0 indicate affinity, values below indicate avoidance.

Electivity analysis for the winter period showed that female *M. mustelus* actively avoided temperatures colder than 15 °C and temperature warmer than 18 °C. Between those temperature values, electivity values switched from avoidance to affinity. For males, electivity analysis suggests a preference between 15 °C and 17°C, with a strong avoidance of temperatures above 17°C (Figure 4.11).

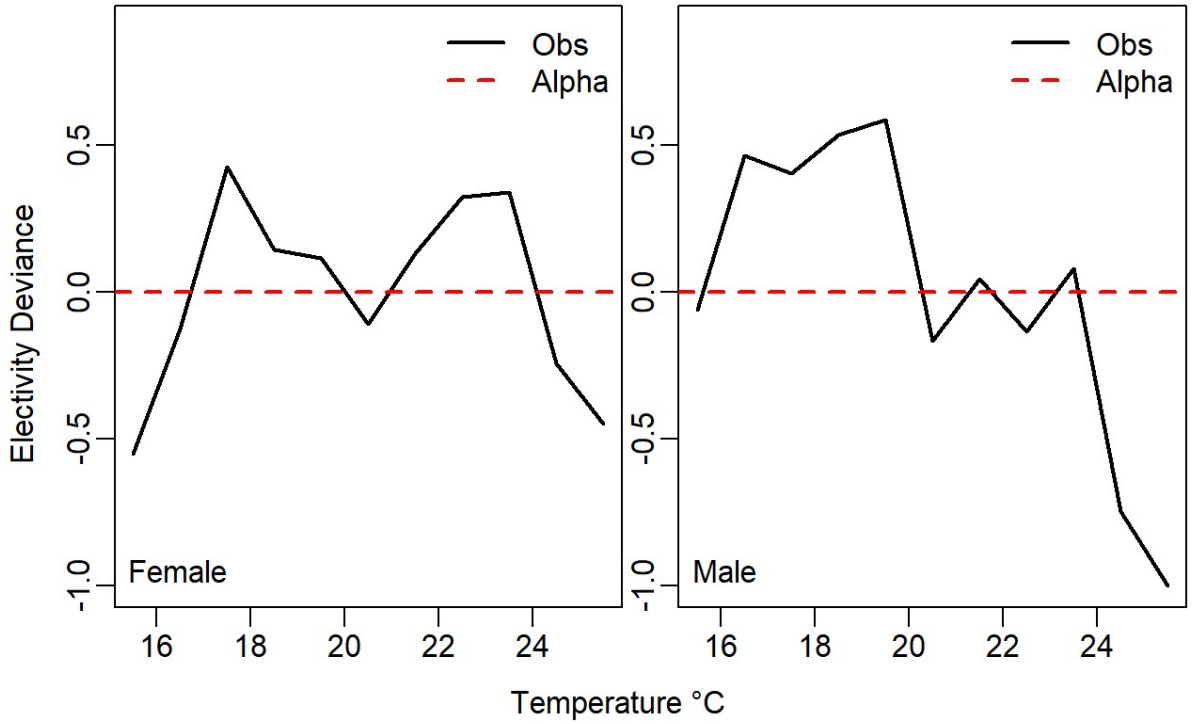


Figure 4.12. Temperature electivity analysis for *M. mustelus* in summer, showing the electivity values standardized by the value of Chesson's α (electivity deviance); values above 0 indicate affinity, values below indicate avoidance.

Electivity analysis for the summer period showed that female *M. mustelus* actively avoided temperatures colder than 17 °C and temperature warmer than 24 °C. Between those temperature values, electivity values switched from avoidance to affinity. For males, electivity analysis suggests a preference between 17 °C and 20°C, with a strong avoidance of temperatures above 24°C (Figure 4.12).

Combined effects of abiotic factors on movement

The results of GAMMS that were used to test the combined effects abiotic factors on movement and direction of movement are summarised in Tables 4.10-13. Models 2-6 had similar AIC and BIC values, but the lowest combination of AIC and BIC emerged from model 3 (Table 4.10). Collectively, the following variables could at best explain only 4.3% of the variation in probability of movement in descending order: *delta temperature*, *absolute temperature*, *diel period* and *moon* (Table 4.11). The addition of shark id as a random effect was did not improve AIC and BIC values, was not significant and was therefore removed during pre-selection of models. Therefore, the probability of movement was best described by a combination of *delta temperature, absolute temperature* and *diel* period. Manual backwards selection was used to test the significance and importance of each parameter (Table 4.11).

The final model describing movement of *M. mustelus* between time intervals was best described by:

$$logit(p) = \beta_0 + f_1(dT) + f_2(abs.T) + diel \quad [8]$$

To predict the influence of individual predictor variables on the probability of movement, a reference set of standardized conditions was constructed by setting *abs. T* and *dT* to the median. Predictions were completed for the following; *abs. T* and *dT* predicted for each diel cycle (Figures 4.13-4.14).

Figure 4.13 predicts the probability of a shark moving over a range of *absolute temperatures*. When the temperature was between 18 and 22 ˚C there is a lower probability of movement.

This response is modified during time of day, at night sharks are more likely to move regardless of temperature. Movement probability is less at 22 ˚C for all diel periods.

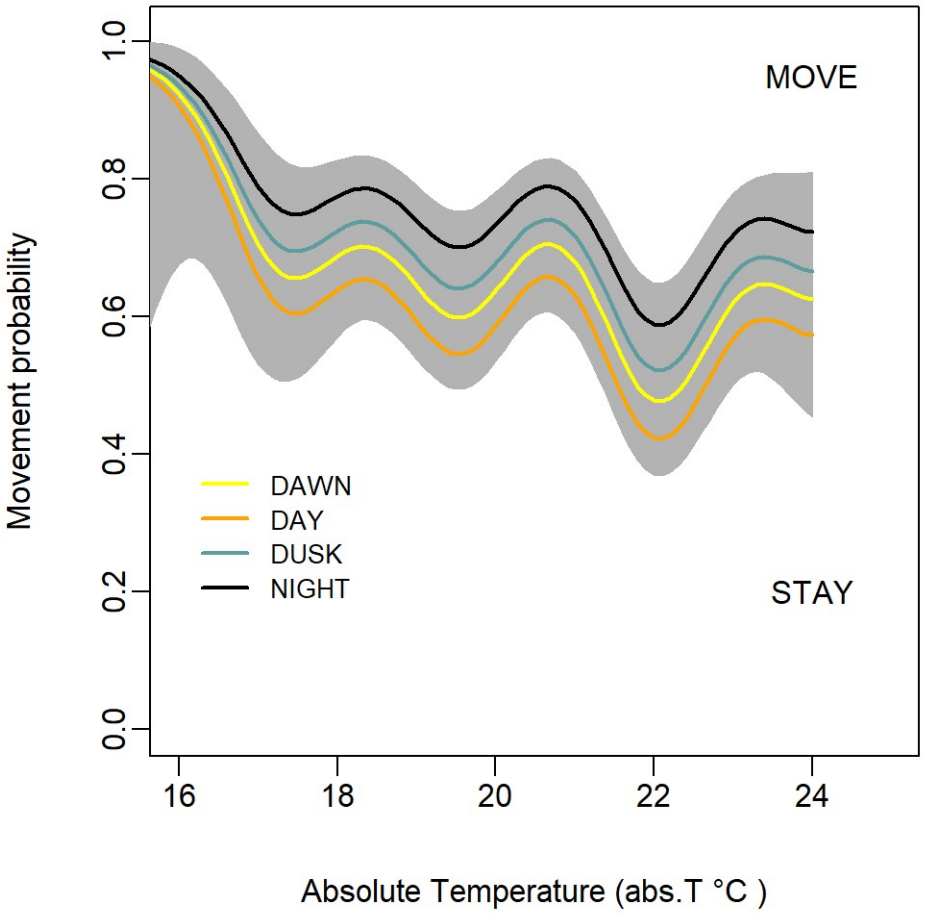


Figure 4.13. Model predictions for the movement probability in relation to *abs. T* and *diel cycle* with fixed *dT*. Confidence intervals of the GAMM predictions shown in grey.

Figure 4.14 predicts the probability of an animal moving over a range of *delta temperatures* (*dT*). When the water gets warmer, sharks tend to remain in the same position. As water temperature decreases they tend to move. This response is modified during time of day, at night sharks are more likely to move regardless of temperature change.

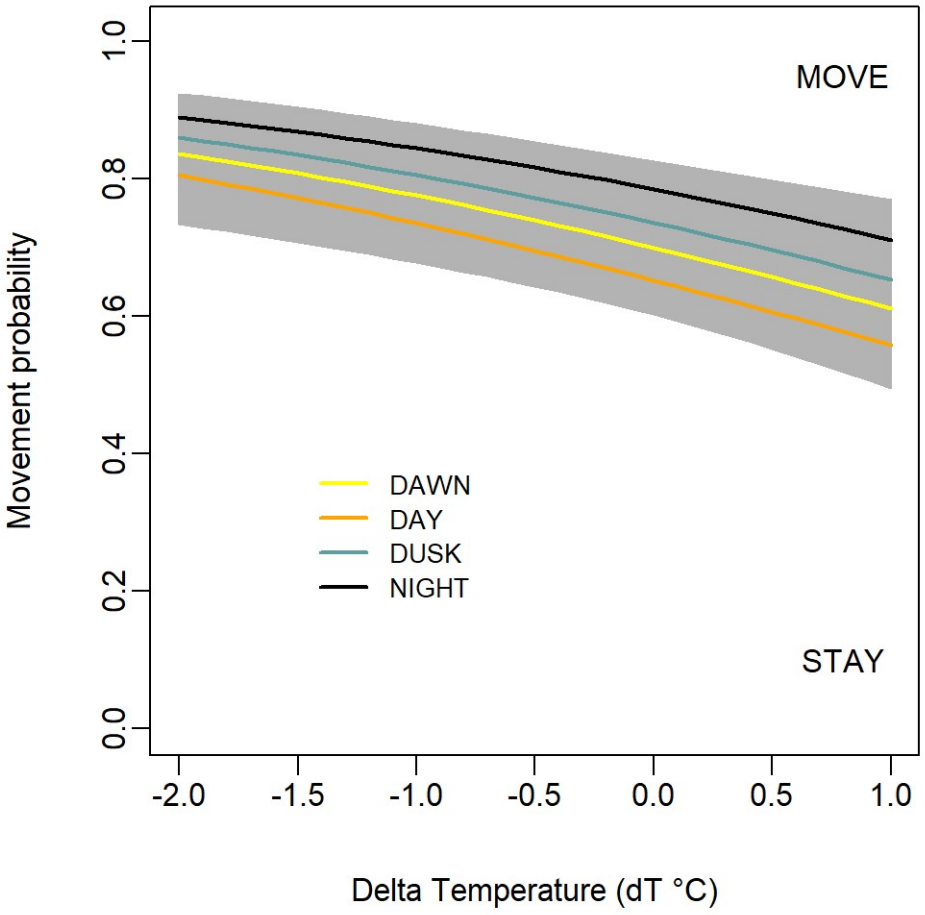


Figure 4.14. Model predictions for the movement probability in relation to *dT* and *diel cycle* with fixed *abs. T* . Confidence intervals of the GAMM predictions shown in grey.

Table 4.10 GAMMs used to analyse the environmental effects on binary movement data, with summary of AIC and degrees of freedom

	Model	df	AIC	BIC	%Dev	Chi^2
1	$logit(p) = \beta_0 + f_1(abs.T)$	9.00	3054.58	3106.51	1.33	**<0.001**
2	$logit(p) = \beta_0 + f_1(abs.T) + diel$	11.77	2995.57	3063.51	3.43	**<0.001**
3	$logit(p) = \beta_0 + f_1(abs.T) + diel + f_2(dT)$	12.70	2982.25	3055.56	3.92	**<0.001**
4	$logit(p) = \beta_0 + f_1(abs.T) + diel + f_2(dT) + f_3(moon)$	14.35	2975.35	3058.23	4.26	**<0.001**
5	$logit(p) = \beta_0 + f_1(abs.T) + diel + f_2(dT) + f_3(moon) + tide$	15.25	2975.03	3063.12	4.33	**0.13**
6	$logit(p) = \beta_0 + f_1(abs.T) + diel + f_2(dT) + f_3(moon) + flow$	15.37	2077.23	3065.99	4.27	**0.66**

Table 4.11 Summary statistics for covariates used in the final binomial GAMMs fitted to probabilities of *M. mustelus* moving between positions during time intervals

Covariate	p-value	Percentage of deviance explained	r^2
dT	<0.001	2.10	**0.02**
abs.T	<0.001	1.33	**0.03**
diel	<0.001	0.49	**0.03**

Despite the difficulty in predicting the probability of movement, greater success was achieved in predicting the direction of movement. Models 8-10 had similar AIC and BIC values, but the lowest combination of AIC and BIC emerged from model 8 (Table 4.12). Collectively, the following variables explained 42.7% of the variation in direction of movement in descending order: *delta temperature* (24.90%), *absolute temperature* (7.04%) and *diel period* (5.72%) (Table 4.13). Therefore, the direction of movement was best described by a combination of *delta temperature, absolute temperature* and *diel* period.

Tide and *moon* was not significant and was subsequently dropped from the model. Therefore, the model that best explains the effect of environmental conditions on a *M. mustelus* swimming in a particular direction is given as:

$$logit(p) = \beta_0 + f_1(dT) + f_2(abs.T) + Diel \quad [9]$$

To predict the influence of individual predictor variables on the probability of a *M. mustelus* moving in a particular direction, a reference set of standardised conditions were constructed by setting absolute temperature to the median, *delta temperature* to the median, area to 1, and

diel period to dusk. Predictions were completed for the following; *delta temperature* and *absolute temperatures* for all *diel periods.* (Figures 4.15-4.16).

Figure 4.15 predicts the probability of an animal moving in a particular direction over a range of temperature changes. When the water gets warmer, sharks move towards Saldanha Bay, when the temperature gets colder they move towards the closed area. This response is modified during time of day, at dawn the probability of moving towards Saldanha Bay increases at colder temperatures.

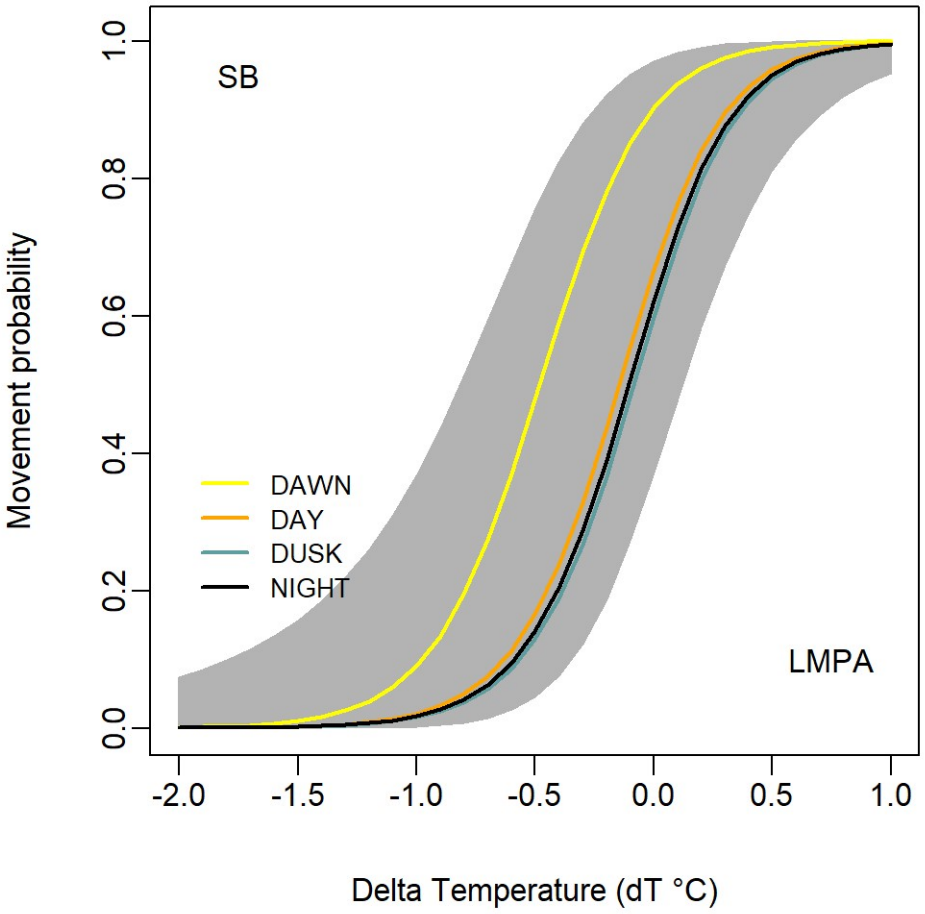


Figure 4.15. Model predictions for the directional movement probability in relation to *dT* and *diel cycle* with fixed *abs.T*. Direction of movement is indicated as SB (Saldanha Bay) or towards the closed area. Confidence intervals of the GAMM predictions shown in grey.

Figure 4.16 predicts the probability of an animal moving in a particular direction over a range of *absolute temperatures*. When the water temperature is lower than 20˚C, there is a high probability of sharks moving towards Saldanha Bay. This response is modified during time of day, at dawn this effect occurs at warmer temperatures, however overall the probability of movement towards the closed area remains low.

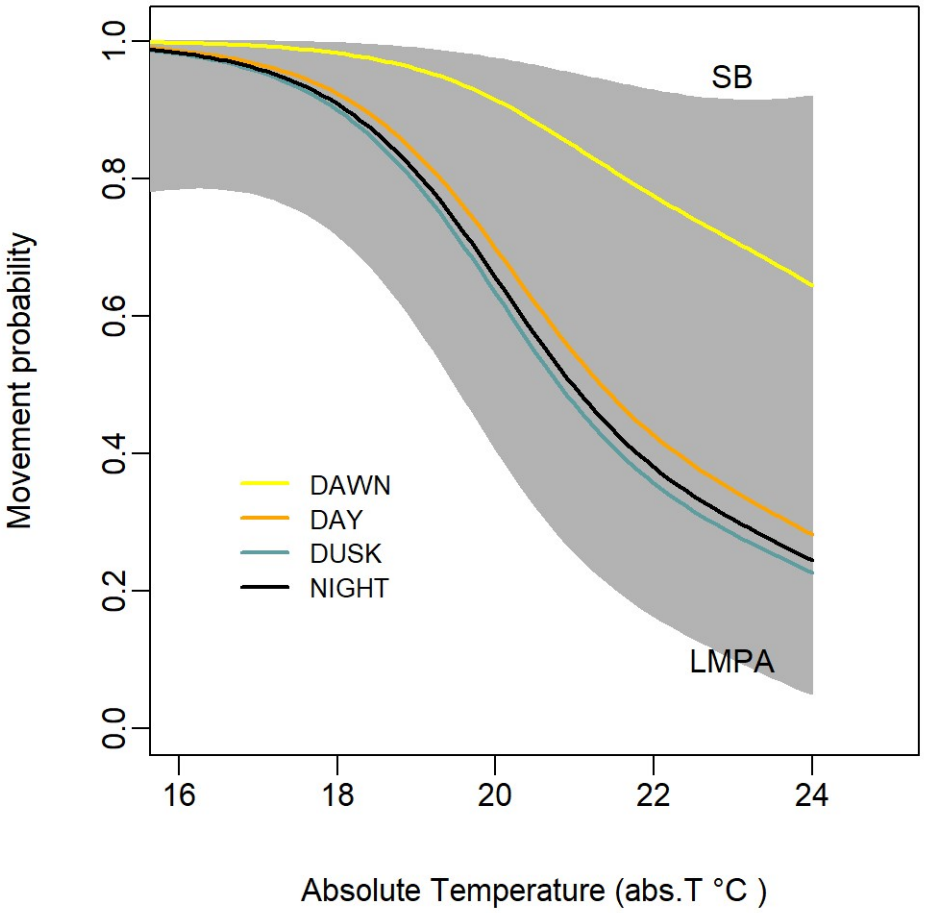


Figure 4.16. Model predictions for the directional movement probability in relation to *abs.T* and *diel cycle* with fixed *dT*. Direction of movement is indicated as SB (Saldanha Bay) towards the closed area. Confidence intervals of the GAMM predictions shown in grey.

Table 4.12 GAMM Models used to determine the importance of environmental effects on fish direction, with summary of AIC and degrees of freedom

	Model	df	AIC	BIC	% Dev	Chi^2
6	$logit(p) = \beta_0 + f_1(\text{abs. T})$	3.05	222.56	232.18	7.04	**<0.001**
7	$logit(p) = \beta_0 + f_1(\text{abs. T}) + diel$	6.11	215.92	235.24	12.50	**<0.01**
8	$logit(p) = \beta_0 + f_1(\text{abs. T}) + diel + f_2(dT)$	8.04	149.56	174.95	42.7	**<0.001**
9	$logit(p) = \beta_0 + f_1(\text{abs. T}) + diel + f_2(dT) + f_3(moon)$	8.04	149.56	174.96	42.7	**<0.01**
10	$logit(p) = \beta_0 + f_1(\text{abs. T}) + diel + f_2(dT) + f_3(moon) + tide$	9.10	150.98	179.68	43.00	0.43

Table 4.13 Summary statistics for covariates tested in the binomial GAMMs fitted to probabilities of *M. mustelus* moving different directions during time intervals

Covariate	F-test	p-value	Percentage of deviance explained	r^2
dT	3.42	**<0.001**	28.8	0.30
abs.T	3.25	**0.001**	9.43	0.1
diel	2.88	**<0.001**	2.8	**0.03**

DISCUSSION

Abiotic conditions in the closed area

Saldanha Bay represents an ecologically unique area, with environmental conditions completely different to that of the neighbouring Atlantic Ocean (Shannon and Stander, 1977). While the Benguela Current running along the west Coast of southern Africa, is composed of cool upwelled water, the water inside the shallow bay is heated by solar radiation, particularly in summer. As opposed to other bays in the region, limited water exchange occurs between the Atlantic Ocean and Saldanha Bay, with tidal motion moving the same water mass back and forth (Shannon and Stander, 1977). Therefore, it is to be expected that the habitat inside the embayment as experienced by its residents is fairly warm and sheltered.

The environmental conditions within the Saldanha embayment fluctuates over seasonal, lunar and diel cycles. Moreover, due to geographical features at different locations, at any given time, conditions related to tidal change such as water depth, temperature and strength of tidal current differ predictably among areas within the bay. These spatio-temporally fluctuating environmental conditions influence the individual sharks' decision to either remain within a certain environmental stratum or to relocate to a more favourable one. To understand how and why such decisions are made, it was necessary to collect *in situ* measurements of the most important variables that constitute potential triggers for such a decision. These *in situ* measurements taken over an appropriate time scale and with a resolution high enough to match the position data of the telemetered sharks was necessary to determine the ultimate cause of the fine scale movement of these sharks.

The tidal lag between the Saldanha Bay mouth and the southern-most part of the closed area is *ca.* 70 minutes, but only 30 minutes between the closed area boundary and the southern-

most receiver position in Langebaan Lagoon (Hedger *et al*., 2010). These findings correspond to those from previous studies by Shannon and Stander (1977) although the new measurements were *in situ* and taken continuously with better technology than available at that time.Tidal elevation was higher at the boundary than the southern-most position. This is as a direct result of the tidal inflow that tends to fan out towards the shallower and wider southern-most part of the bay.

In summer, more variation in temperature is seen at the closed area boundary than the southern-most position in the lagoon. In contrast, in winter more variation in temperature is seen at the southern-most position. The closed area or inner lagoon consists of shallow mudflats exposed during low tide with branching channels between 4 and 11 m deep running the length of the lagoon (Shannon and Stander, 1977). The outer lagoon along the closed area boundary is deeper on average and contains few tidal flats (Shannon and Stander, 1977). Therefore, as the water moves into the lagoon and towards the southern-most portion of the closed area it fans the water out against the shallow tidal flats and the deeper channels. In summer, the temperature is warmer close to the southern-most position within Langebaan Lagoon than other positions, as a result of shallow tidal flats being heated by solar radiation.

The locations where the lowest temperatures were measured differ between winter and summer. In winter, the lowest temperature was measured at the southern-most position within the closed area (10.7 ˚C), however, in summer the lowest temperate was measured outside the closed area (12.7 ˚C). The location of the summer minimum is a direct result of wind induced upwelling. In both winter and summer, temperatures were colder during the day at both the southern-most position within the closed area and its boundary.

The temperature in the closed area is subject to periodic changes on different temporal scales. Temperatures measured in this study were similar to average values observed in a previous study at between 14-19 ˚C (Shannon and Stander, 1977). However, measurements made by Shannon and Stander (1977) did not include the area south of the boundary, and were therefore lower than those measured in this study. Measurements from earlier studies were on average 4 ˚C warmer than the inshore surface temperature along the West Coast. Although average summer temperatures were 6˚ C higher than those in winter, rapid temperature changes of up to 12 ˚C within one day, driven by tide and solar radiation, occurred at a single position. Daily variations may therefore have been larger than seasonal variation in summer. Shannon and Stander (1977) showed a 2 ˚C difference between January (summer) and July (winter) conditions.

A shallow thermocline is present at deeper stations in Saldanha Bay in summer and autumn, with temperatures decreasing to below 10 ˚ C (Clarke *et al.*, 2017). As there were no instruments placed in the area, the effects on shark movement is unknown. However, the water below the thermocline is outside the thermal preference for *M. mustelus* according to our study and confined these bottom dwelling sharks inside the LMPA. In winter, warm water was not available anywhere with no thermocline present as a result of strong wind driven vertical mixing (Clarke *et al.,* 2017). Therefore, the water column between the closed area and Saldanha Bay was more uniform.

From August to May higher temperatures were measured at the southern relative to the northern-most station, due to the shallower water body being heated more rapidly by solar heating. The north-south temperature gradient breaks down in May. Seasonal temperature explains the variation in the temperature explained the seasonal movement of *M. mustelus.* Results from the telemetry study showed that sharks were concentrated within the closed area closed area in summer (within positions C3 to LW) and that movement in the form of boundary crossings was strongly influenced by season (Chapter 3). During autumn, winter and early spring, sharks are dispersed more widely across Saldanha Bay and beyond, whereas only a few outings outside the closed area occurred during summer. Although the majority of sharks remained inside the bay, two sharks left Saldanha Bay in the second week of May 2007 at the same period when the difference in temperature between the southern-most and northern-most positions inside the closed area decreases. No sharks left Saldanha Bay in summer. This seasonal pattern of sharks moving inshore in summer and offshore in winter has been observed in other Triakid sharks including *M. antarcticus, M. henlei* and *M. californicus* (Barnett and Semmens, 2012: Hopkins and Cech, 2003, Espinoza *et al.*,2011). However, none of these studies evaluate movement based on *in situ* measurements of temperature and comparisons might not be valid.

General fine scale movement patterns of *Mustelus mustelus*

This study, examined the fine scale movement patterns of *M. mustelus.* The individual plots of telemetered individual sharks revealed consistent, regular movements up and down the channels within the closed area with limited and occasional forays away from these channels.

Movements were largely restricted to a small (1.91 km^2) area in the main channel. This corresponds to movements described in Chapter 3. Sharks in general aggregated in the main channels in summer, with multiple sharks at the same positions during the same day (Figure 2.1, Chapter 2). Repeated use of these areas indicates that sharks are familiar with these areas and navigate back and forth between preferred sites. Since these sites have high densities of preferred prey species (Chapter 2), this suggests that the distribution of *M. mustelus* might be partially linked to the distribution of prey. However, while foraging on the sandbanks, sharks were likely out of range of receivers moored along the channels. This was highlighted in Chapter 3 as relatively low number of individual sharks were detected daily compared to the actual numbers of individual sharks in the system. Several studies have suggested that shallow mudflats are essential habitats for sharks in estuarine environments (Ackerman *et al.*, 2000; Campos *et al*., 2009). None of these sharks visited the southern-most positions of the lagoon (C1 and C2), but were frequently recorded at other positions inside Langebaan Lagoon. The southern-most area is likely avoided due to temperatures of higher than 25 ˚C in summer during the day or may be too shallow for larger sharks.

Although the telemetered sharks made use of similar areas (Chapters 3 and 4) and exhibited regular movement patterns there was little evidence for synchronicity in the movement on both the 20-minute and the one-hour resolution. This lack of synchronous movement by *M. mustelus* may be an artefact of small sample size (number of tagged sharks with data = 15). A detailed investigation into movement synchronicity and schooling behaviour was beyond the scope of this study. Movement observed in Chapters 3 at least on a day resolution suggests some degree of aggregating behaviour. *Sphyrna lewini* is one of the few shark species where highly organized schooling behaviour has been described in the literature (Klimley and

Nelson 1981, Klimley, 1985). However, grouping in large numbers (Jacoby *et al.*, 2012) and or aggregating (Dewar *et al*., 2008; Economakis and Lobel, 1998; Heupel and Simpfendorfer, 2005) are behaviours well known in elasmobranchs. The drivers of shark aggregations are well studied. They include reproduction (Harris, 1952; Olsen, 1954), conservation energy resources (Klimley and Nelson, 1984; Sims *et al*., 2006b), feeding purposes (Wallman and Bennett, 2006) and avoidance of predators (McKibben and Nelson, 1986).

Fine scale movements and environmental factors

The preference of *M. mustelus* for certain areas along the main tidal channel and the regularity and repetitive nature of movement tracks indicates that these movements might be triggered by a periodical change in the environment *i.e.* a change in tide, temperature or diel cycle. The thermal preference of *M. mustelus* as determined by GAMMS and electivity analysis is between 18 to 22 ˚C in summer. Once the temperature in the immediate surrounding becomes warmer or colder than this range, the animals adjust their position according to the gradient, to remain within their preferred temperature envelope.

Analysis and examination of individual temperature where sharks occurred from histograms showed a considerable degree of variability of up to 2 °C among individual sharks. Generally, in winter the majority of sharks occurred in water warmer than the average ambient temperature. In summer, sharks occurred in temperatures colder than the average ambient temperature. In winter, the temperature at which sharks spent their time was on average 16 °C, in summer this temperature was on average 20 °C. The temperature in which sharks occurred (Figures 4.8-4.9) in summer was within the temperature preference predicted

by GAMMS (18-22 °C). It was not possible to use GAMMS to determine the temperature thresholds in winter that determine when or how *M. mustelus* move. However, given that the temperature in which sharks occurred in summer (20 °C) was within the thermal preference range predicted by GAMMS, it is likely that real thermal preference in winter is around 16 °C.

For both winter and summer there was a significant difference in the temperature sharks occurred in between sex and maturity state. Females were found in warmer water than males in both winter and summer. Similarly, females showed a stronger preference for warmer water than males. Immature sharks were found warmer water in winter than mature sharks, while in summer the opposite trend was observed. Temperature selection by *M. mustelus* is similar to those observed in *M. canis* (Casterlin and Reynolds, 1979) and teleost fish (DeWitt and Friedman, 1979), with a single preferred, modal temperature. This modal temperature is likely to be the optimal temperature where physiological rates such as metabolism, growth and digestion are optimized (Sims *et al*., 2006b; Wallman and Bennett, 2006). Telemetry studies suggest that elasmobranchs found in thermally heterogeneous environments will feed in warmer waters and rest in cooler waters (Sims *et al*., 2006b). The warmest temperatures are experienced within the closed area where animals spend a large proportion of their time in spring and summer (Chapter 3), coldest temperatures are also experienced inside the closed area in winter. Advantages gained from behavioural thermoregulation are negated under conditions where temperature regime falls out of the optimal thermoregulatory temperature range (Sims *et al*., 2006b).

Females occurred in warmer temperatures than males during winter and summer periods. The reproductive cycle investigated in Chapter 2 describes an 11-month gestation period starting in summer. Females may prefer warmer water to increase both gastric efficiency and increase growth rates of embryos, as previously described for *T. semifasciata* (Hight and Lowe, 2007), *Prionace glauca* (Carey and Scharold, 1998) and *Myliobatis californica* (Matern *et al.*, 2000). Neonates and juveniles increase their growth rates while pregnant females increase the growth rate of developing young and decrease gestation periods (Harris, 1952). As with most elasmobranchs female *M. mustelus* mature at a larger size than males. Warmer waters increase metabolic rates increasing growth rates (Hight and Lowe, 2007), in the absence of resident predators and abundant food. As females occurred in and preferred warmer temperatures it is likely that these movement patterns are explained by thermoregulation. The hypothesis has been tested in laboratory conditions where embryonic *Scyliorhinus canicula* grew significantly faster in warmer waters (Harris, 1952). It is likely that *T. semifasciata* aggregate in warm waters to increase body temperature which increases the growth rate of embryos resulting in a shorter gestation period (Hight and Lowe, 2007).

Movement of immature sharks may be as a result of predator avoidance. There are no resident predators of *M. mustelus* in the closed area, although Carcharhinids and *N. cepedianus* enter the closed area seasonally (da Silva, unpublished data). As movement of other triakids have been shown to be heavily influenced by predators, it is possible that the combination of deeper channels and shallow flats inside the closed area offer a refuge from predators (Ackerman *et al*., 2000, Barnett *et al*., 2010; Barnett *et al*., 2013; Campos *et al*., 2009, Ezpinoza *et al*., 2011).

GAMMS showed that the probability of movement in summer was significantly affected by absolute temperature, changing temperature and diel cycle. The final model explained only 4.35% of the deviance, this is not surprising given that there are a multitude of factors that may explain the decision a shark makes to move from one position to another. Some inferences were made in the initial data preparation phase that may have affected these results, including binning of telemetry data into 20-minute intervals. However, since *M. mustelus* sampled in this study are relatively large, they are able to move freely between positions within that time period.

Sharks are less likely to move when the water temperature is between 18 and 22 ˚C, at warmer and colder temperatures the probability of sharks moving to different positions is increased. When the water gets colder, sharks are more likely to move than if the water gets warmer. At night sharks are more likely to move, regardless of temperature or temperature change. However, this "basin" effect could be an artefact of the data range, since few data points at either extreme has been recorded. Once the decision to move was made by the shark, the probability of movement in a particular direction was significantly affected by absolute temperature, the magnitude of change in temperature and diel cycle. The final model explained 42.7% of the deviance and these factors can be considered important drivers on the decisions animals make on directional movement towards Saldanha Bay and the closed area. Most of the deviance was explained by adding the term *delta temperature*, which can be considered as a measure of the cooling or warming that the shark experiences at the position it departs from. This environmental stimulus is likely the trigger for the sharks' position adjustment. As water temperature increases outside the 18 - 22 ˚C range as determined by GAMMS sharks move towards Saldanha bay. As elucidated in chapter 3 the sharks

movements included the entire bay, therefore one might assume that their knowledge of their larger area of residence will influence the choice of movement direction. Another plausible explanation is that sharks simply moves according to the direction of the change in the temperature gradient: Warming and cooling is partly confounded with the in- and outflow of the tide.

The diel cycle affects movements of *M. mustelus* in the LMPA. Sharks were more likely to move at night regardless of environmental conditions. Many different species of shark with widely different foraging strategies have been shown to undertake diel movements including *Carcharhinus amblyrhynchos* (McKibben and Nelson, 1986), *Negaprion brevirostris* (Gruber *et al*., 1988) and *Megachasma pelagios* (Nelson *et al*., 1997). These sharks moved greater distances during dark periods such as night and new moon. *T. semifasciata* have shown similar movements with an increased distance moved at night (Ackerman *et al.*, 2000). Similarly, juvenile *S. lewini* used a small core daytime area, ranging widely at night foraging for food (Holland *et al*., 1993). Many different triakids have been shown to be nocturnal including the *Mustelus canus* (Rountree and Able, 1996) and *M. californicus* (Barnett *et al*., 2010).

Conclusion

The investigation of the fine scale movement of M. mustelus in Saldanha bay revealed consistent, and at least to a certain degree, predictable relationships between a shark's decision to move and its choice of direction and the change in ambient conditions. Whereas the tidal cycle had surprisingly little measurable influence, the distribution and change of the

water temperature in the area, which is a function of solar radiation, particularly in the shallow southern part of the Lagoon had a significant effect and accounted for most of the deviance explained in the models. A feature of the bay is a strong temperature gradient from the sea to the top of the lagoon, which may span a range from 10 to 26 ˚C. Tidal currents, winds and seasons change the water temperature on a daily, weekly and seasonal basis. It is primarily the changing temperature that influences the movement of *M. mustelus* in Saldanha Bay. In particular, the avoidance of warm and cold water outside their thermal preference causes the most predictable movement.

CHAPTER 5: CONCLUSIONS

The process of conducting a stock assessment for a fishery resource involves the simplification of complex processes (Quinn and Deriso, 1999). Most stock assessment models assume homogenous stock structure, randomly and evenly distributed in space and time. This assumption holds for very few marine animals (Ricker, 1958; MacCall, 1990). Whereas some of the bias in abundance estimates is removed by way of Catch per Unit Effort (CPUE) standardisation, movement patterns and spatial distribution of catch are considered in only the most sophisticated models for the most valuable stocks, albeit in a simplified from (Goethel *et al.*, 2011). Questions around stock delineation have not been satisfactorily resolved for the majority of marine species, yet stock boundaries and stock structure are known to have potentially large effects on assessments, especially for species for which some data exists (Goethel *et al*., 2011). For example, the movement of *Isurus oxyrinchus* across the boundary (20 ° longitude) between ICCAT and IOTC jurisdictions has a substantial effect on annual catch, and in turn on regional assessments, yet it is not incorporated in any of the assessment models (Parker *et al.*, 2017).

Southern African *Mustelus mustelus* are genetically structured into two stocks with the Atlantic and Indian Ocean boundary restricting gene flow (Maduna *et al*., 2016; Maduna *et al*., 2017). Local differences in pigmentation, growth, fecundity and diet evident in this study corroborated that finding. Complex movement patterns of *M. mustelus* across several spatial and temporal scales, driven by changes in the environment and season were also revealed. The development of a full, dynamic assessment that accounts for this variability in movement

patterns and existence of two stocks is complex and difficult to justify given that it is a relatively low value species caught on a small scale compared to other fisheries South Africa.

There have been few attempts at assessing chondrichthyan stocks in South Africa, even annual reported landings can be in excess of 3000 t. Consequently, there is a lack of species specific management in South African chondrichthyan fisheries, despite increasing conservation concern for some species. In the absence of effective controls, protection within MPAs in South Africa might provide some insurance against overexploitation and ultimately aid the sustainability of shark fisheries. To fulfil this role, closed areas must include preferred habitat for the target species and be positioned such that these sharks spend a large proportion of their time inside them. The areas used for crucial life-history stages such as mating, pupping and nursery grounds are also suitable sites for closed areas.

The biology of *M. mustelus* in Saldanha Bay

Populations of coastal species are seldom homogenous as they have to adapt to the conditions of an environment under constant flux (Goethel *et al*., 2011). Sharks sampled in the study area were phenotypically distinct from those from four other studied regions and represented *M. mustelus* of the southern Atlantic stock (Maduna *et al.*, 2016). These represented the animals with the largest birth and maximum lengths as well as those with the largest litters. Furthermore, sharks from the area were distinct in their diet and pigmentation. The diet of *M. mustelus* in the lagoon consisted of predominantly three species of crustaceans; *Hymenosoma orbiculare*, *Upogebia africana* and *Callichirus kraussi*. Unlike other regions, no ontogenetic shift in diet was observed for the Langebaan Lagoon *M. mustelus*. As the diet does not

change with size and prey items are common and small, it is likely that the habitat of neonate, juvenile and adult *M. mustelus* are similar, with similar seasonal shifts. If foraging patterns are similar throughout the population structure for *M. mustelus* the protection provided by the closed area in summer should extent to all size classes, which included some of the largest, most fecund animals sampled from this species. The closed area provides a nursery ground for *M. mustelus* based on the criteria developed by Heupel *et al.*, (2007). Firstly, that neonate and juvenile sharks are more commonly found within the closed area than outside. Secondly that these sharks remained inside the closed area for extended periods and lastly that the area was used repeatedly over a number of years. In addition, the presence of neonates, juveniles and ovulating, pregnant and post-partum females inside the closed area confirms that the closed area constitutes preferred habitat for all life-history stages of *M. mustelus.* These critical life-history stages occur in summer, which coincides with the highest level of fishing pressure outside the closed area.

Can a coastal MPA protect a commercially fished shark population?

The work here negates the assumption of homogenous distribution in space and time. *M. mustelus* exhibit seasonal spatio-temporal behaviour with summer residency inside the closed area and winter movement into Saldanha Bay and out into the Atlantic Ocean.

Movement from the Langebaan Lagoon closed area to other neighbouring regions may play a role in supplementing outside targeted populations but only as far as the Indian Ocean boundary as gene-flow has been shown as unidirectional to the west (Maduna, 2016). Therefore, even a small closed area potentially has a disproportionately large effect on overall sustainability. This study quantified the degree of protection in terms of percentage of time

sharks spent inside the closed area with the intention of identifying unique characteristics that can be extrapolated to other closed areas and other coastal shark populations. Sharks spent an average of 79% of their time inside the closed area which represents only 35% of the entire bay. A combination of shallow and sheltered waters in close proximity to the Saldanha Bay port and other boat-access points with an increase in fishing effort in summer would normally make the seasonal aggregation highly vulnerable to exploitation. The closed area could be motivated simply on the grounds that these sharks need protection during this vulnerable season. Protection decreased in winter as sharks generally spread themselves across the entire Saldanha embayment. These results indicate that the closed area may still be effective if it was only closed seasonally. Therefore, management interventions for *M. mustelus* in other regions could include aspects of seasonal closure to fishing activities where similar aggregations might occur in accessible waters. As *M. mustelus* do leave the confines of the closed area, they are still accessible to commercial fisheries but only during brief excursions in spring and winter when they disperse across the Saldanha embayment and potentially extend their range into the Atlantic Ocean. The results clearly showed that if strategically placed, MPAs may be effective in protecting coastal shark species in the absence of species-specific management.

How is the movement behaviour of *M. mustelus* affected by environmental conditions?

This work showed that the movement direction of *M. mustelus* inside the Saldanha embayment was predominantly affected by shifting isotherms. The avoidance of warm and cold water outside their thermal preference caused the most predictable movement. Repeated movements of *M. mustelus* across the wide areas suggested that they were familiar with the area and able to navigate between preferred sites. These repeated movements and consistent seasonal movement at least over a two-year time-frame suggests that this familiarity with their environment involves an understanding of where conditions would be more favourable when the water becomes too hot or too cold. Female *M. mustelus* preferred warmer water than males, presumably to benefit the pupping process. Higher temperatures increase growth rates of developing young and decrease gestation periods.

The management implications of the movement behaviour of *M. mustelus* in the Langebaan Lagoon MPA?

This thesis was developed with the view of determining under which biological and ecological conditions an area could be a good candidate for selection as a closed area for a coastal shark population. Although these conditions may also apply to other coastal sharks and even teleosts, these conditions were determined using *M. mustelus* as a model. This study agrees with current literature that for an area to be a good candidate for selection as a closed area it has to encompass the habitat of the species in question so that it spends large proportion of its time within its confines. In summer, *M. mustelus* was confined in a small area inside the closed area with abundant prey within their optimum temperatures. Seasonal movement occurred during winter when they disperse across Saldanha bay and into the

Atlantic Ocean and were therefore no longer protected. It is common for sharks to exhibit seasonal movement, either aggregating or dispersing for feeding, breeding and safety. An area may be suitable as closed area as a candidate if sharks aggregate and spend their time inside its confines on a seasonal basis. However, in such cases the use of seasonal closure as a management intervention might be a more practical solution, provided that enforcement of such legislation is not challenging.

For a shark species to spend a large proportion of its time within a closed area, the area should provide adequate high-quality food resources, be reasonably safe from predators and be within the thermal tolerance of the species it is intended protect. An added benefit is if the area is not homogenous to surrounding areas and there is something special about the area that draws sharks there *i.e.* seamounts or atolls.

In terms of biology, an area could be a suitable candidate as a closed area if large and fecund sharks occur and spend significant time within its confines. *M. mustelus* increase in fecundity with size, with larger females giving birth to larger offspring and generally as a pure consequence of size, pups may have increased survival rates. *M. mustelus* has a high natural mortality before 50% maturity, therefore having the large females inaccessible to fishers at least on a seasonal basis is beneficial. Alternatively, an area could be a suitable candidate as a closed area if it could provide protection to the nursery. Increased protection would also be provided if crucial life-history stages such as ovulation, mating and parturition occur within the confines of the closed area.

This study highlighted the importance of temperature to the occurrence of a coastal shark species inside a closed area. The presence of sharks inside the closed area and movement away from it was directly linked to temperature. An important feature worth considering when a closed area is implemented or planned is whether the thermal environment for the species in question falls within the optimum thermal preference for at least large portions of the year. However, if such conditions only occur seasonally for a number of species, a seasonal closed area could be considered. Such an area could be a good candidate for a closed area if it offers thermoregulation benefits such as increased growth, decreased gestation period but also could provide a thermal refuge.

It is worth noting that the impact of climate change on the movement behaviour of this coastal shark could be considerable. As a result of the thermal preferences, changes in water temperature could result in a range shift towards areas outside the closed area (such as winter dispersal), where there is no protection from fishers during the period when these sharks aggregate. Such changes in movement behaviour as a result of changing temperature is possible for all chondrichthyans and needs to be considered within the frameworks of current closed areas and those under consideration. Furthermore, the temperature preferences of chondrichthyans and related impact of climate change need to be studied in terms of movement biology to best understand potential consequences.

Synthesis

Overall, this thesis has made several contributions to our knowledge of the movement coastal shark species, particularly in the context of protection provided by closed areas. This study showed that the coastal shark species: *Mustelus mustelus* from Langebaan Lagoon are

phenotypically distinct from other studied regions in terms of differences in pigmentation, growth, fecundity and diet. They exhibit complex movement patterns across several spatial and temporal scales, driven by environment and seasonal changes. *Mustelus mustelus* show a high level of residency to the closed area inside Langebaan Lagoon. Therefore, they receive a large degree of protection from fishing activities. Additionally, several crucial life-history stages occurred within the Langebaan Lagoon closed area including pupping, nursery and feeding grounds at all sizes. The combination of sheltered warm waters, rich feeding grounds and the protective effect of the closed area may explain the high abundance and occurrence of the largest *M. mustelus* globally. This work shows that a closed area could provide a large degree of protection to a coastal shark species if it is strategically placed within favourable environmental conditions, where the shark is highly abundant and where several crucial life-history stages take place within its boundaries.

REFERENCES

Abrantes, K.G. and A. Barnett. 2011. Intrapopulation variations in diet and habitat use in a marine apex predator, the broadnose sevengill shark *Notorynchus cepedianus*. *Marine Ecology Progress Series*. 442:133–148.

Ackerman, J. T., Kondratieff, M. C., Matern, S. A., and J.J. Cech. 2000. Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. *Environmental Biology of Fishes*, 58, 33–43.

Adams, S.B. and C.A. Frissell 2001. Thermal habitat use and evidence of seasonal migration by rocky mountain tailed frogs, *Ascaphus montanus*, in Montana. *Canadian Field-Naturalist*. 115:251–256.

Alerstam, T. 1990. *Bird Migration*. Cambridge University Press.

Andrews, A.H., Natanson, L.J., Kerr, L.A., Burgess, G.H. and G.M. Cailliet. 2011. Bomb radiocarbon and tag-recapture dating of sandbar shark (*Carcharhinus plumbeus*). *Fishery Bulletin*. 109(4):454–465.

Andrews, K.S., Williams, G.D, Farrer, D., Tolimieri, N., Harvey, C.J., Bargmann, G., and P.S. Levin. 2009. Diel activity pattern of sixgill sharks, *Hexanchus griseus*; the ups and downs of an apex predator. *Animal Behaviour*, 78; 525-536

Attwood, C.G. and P.D. Cowley. 2005. Alternate explanations of the dispersal pattern of galjoen *Dichistius capensis*. *African Journal of Marine Science*. 27(1):141–156.

Attwood, C.G., Cowley, P.D., Kerwath, S.E., Næsje, T.F., Økland, F. and E.B. Thorstad. 2007. First tracking of white stumpnose *Rhabdosargus globiceps* (Sparidae) in a South African marine protected area. *African Journal of Marine Science*. 29(1):147–151.

Baker, R.R. 1978. *The Evolutionary Ecology of Animal Migration*. London: Stoughton.

Barham, W.T. and Schwartz, F.J. 1992. Physiological responses of newborn smooth dogfish, *Mustelus canis*, during and following temperature and exercise stress. *The Journal of the Elisha Mitchell Scientific Society*. 108:64–69.

Barker, M.J. and V. Schleussel. 2005. Managing global shark fisheries: suggestions for prioritizing management strategies. *Aquatic Conservation: Marine and Freshwater Ecosystems.* 15:324–347.

Barnett, A., Abrantes, K. G., Stevens, J. D., Bruce, B. D., and J.M. Semmens. 2010. Fine-scale movements of the broadnose sevengill shark and its main prey, the gummy shark. *PloS One*, 5(12): e15464. http://doi.org/10.1371/journal.pone.0015464

Barnett, A., Stevens, J.D., Frusher, S.D. and J.M. Semmens, 2010. Seasonal occurrence and population structure of the broadnose sevengill shark *Notorynchus cepedianus* in coastal habitats of south-east Tasmania. *Journal of Fish Biology*. 77(7):1688–1701.

Barnett, A., Abrantes, K.G., Stevens, J.D. and J.M. Semmens. 2011. Site fidelity and sex-specific migration in a mobile apex predator: implications for conservation and ecosystem dynamics. *Animal Behaviour*. 81(5):1039–1048.

Barnett, A. and J.M. Semmens. 2012. Sequential movement into coastal habitats and high spatial overlap of predator and prey suggest high predation pressure in protected areas. *Oikos*. 121(6):882–890.

Barnett, A., Abrantes, K. G., Seymour, J., and R. Fitzpatrick. 2012. Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. *PloS One*, *7*(5): e36574. http://doi.org/10.1371/journal.pone.0036574

Barnett, A., Yick, J., Abrantes, K., and C. Awruch. 2013. Trophic ecology of an abundant predator and its relationship with fisheries. *Marine Ecology Progress Series*, 494, 241–248. http://doi.org/10.3354/meps10577

Bass, A.J., D'Aubrey, J.D., and N. Kistnasamy. 1975. Sharks of the east coast of South Africa. 3. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. *Investigitave Report. Oceanographic Research Institute South Africa.* 38:1-100

Beamish, R.J. and D.A. Fournier. 1981. A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences*. 38(8):982–983.

Bennet, R.J. 2004. Age and growth of the smoothhound shark *Mustelus mustelus* from South Africa, with a note on the effectiveness of alizarin red S for long-term age determination studies of Elasmobranchs. Honours Thesis, Rhodes University, Grahamstown, South Africa

Bennett, B.A. and C.G. Attwood. 1991. Evidence for recovery of a surf-zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa. *Marine Ecology Progress Series*. 75(2/3):173–181.

Blackhart, K., Stanton, D.G. and Shimada, A.M., 2006. *NOAA Fisheries Glossary*. United States Department of Commerce, National Oceanic and Atmospheric Administration.

Block, B.A., Dewar, H., Farwell, C. and E.D. Prince. 1998. A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proceedings of the National Academy of Science,USA*. 95:9384–8389.

Bond, M.., Babcock, E.A., Pikitch, E.K., Abercrombie, D.L., Lamb, N.F. and D.D. Chapman. 2012. Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier Reef. *PloS one*. 7(3):e32983. DOI: 10.1371/journal.pone.0032983.

Bone, Q. and R.H. Moore. 2008. Reproduction and Life Histories. In *Biology of Fishes*. 3rd ed. Q. Bone and R.H. Moore, Eds. New York, USA: Taylor and Francis Group. 217–254.

Bonfil, R. 1994. Overview of world elasmobranch fisheries. *FAO Fisheries Technical Report* 341.

Bonfil, R. 1999. Marine protected areas as shark fisheries managment tool. In *Proceedings of the 5th Indo-Pacific fish conference*. Seret B and J.-Y. Sire, Eds. Noumea, New Caledonia: Societe Francaise d'Ictyologie, Paris and Istitut de Recherche pour le Developpement, Paris. 217–230.

Bonfil, R., Meyer, M., Scholl, M.C., Johnson, R., O'Brien, S., Oosthuizen, H., Swanson, S., Kotze, D. and M. Paterson. 2005. Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science*. 310:100–103.

Bonham, K., F. B. Sanford, W. Clegg and G. C. Bucher. 1949. Biological and vitamin A studies of dogfish (*Squalus suckleyi*) landed in the State of Washington. Washington Department ofFisheries. *Biological Report* 49A, 83-1 14.

Booth, A.J., Foulis, A.J. and M.J. Smale. 2010. Age validation, growth, mortality, and demographic modeling of spotted gully shark (*Triakis megalopterus*) from the southeast coast of South Africa. . *Fishery Bulletin*. 109(1):101–112.

Botsford, L.W., Micheli, F. and A. Hastings. 2003. Principles for the design of marine reserves. *Ecological Applications*. 13(1):S25–S31.

Bradshaw, C.J.A. 2005. Survival of the fittest technology-problems estimating marine turtle mortality. *Marine Ecology Progress Series*. 287(2003):261–262.

Bradshaw, C.J.A., Prowse, T.A.A., Drew, M., Gillanders, B.M., Donnellan, S.C. and C. Huveneers. 2018. Predicting sustainable shark harvests when stock assessments are lacking. *ICES Journal of Marine Science.* DOI: 10.1093/icesjms/fsy031

Brander, K. 1981. Disappearance of the common skate *Raja batis* from the Irish Sea. *Nature*. 290(5801):48–49.

Brouwer, S.L., Griffiths, C.L. and M.J. Roberts. 2003. Adult movement and larval dispersal of *Argyrozona argyrozona* (Pisces: Sparidae) from a temperate marine protected area. *African Journal of Marine Science*. 25(1):395–402.

Buckland, S.T. 1984. Monte Carlo confidence intervals. *Biometrics*. 811–817.
Byrne, R.J. and J.C. Avise. 2012. Genetic mating system of the brown smoothhound shark (*Mustelus henlei*), including a literature review of multiple paternity in other elasmobranch species. *Marine biology*. 159(4):749–756.

Cadima, E.. 2003. *Fish stock assessment manual*. Rome, Italy.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*. 59(2):197–242.

Campana, S.E., Joyce, W., Marks, L., Hurley, P., Natanson, L.J., Kohler, N.E., Jensen, C.F., Mello, J.J., Pratt, Jr, H.L., Myklevoll, S., and S. Harley. 2008. *The rise and fall (again) of the porbeagle shark population in the northwast Atlantic.* Camhi, M.D., Pikitch, E.K., and E.A.

Babcock, *Eds*. Oxford, United Kingdom: Blackwell Publishing. 445:461
Campos, B.R., Fish, M.A., Jones, G., Riley, R.W., Allen, P.J., Klimley, P.A., Cech, J.J. and J. T. Kelly. 2009. Movements of brown smoothhounds, *Mustelus henlei*, in Tomales Bay, California. *Environmental Biology of Fishes*. 85(1):3–13.

Capapé, C. 1974. Observations sur la sexualité, la reproduction et la fécondité de 8 Sélaciens pleurotrêmes, vivipares placentaires des côtes tunisiennes. *Arch. Inst. Pasteur, Tunis*. 51(4):329–344.

Capapé, C., Quignard, J.P. and J. Mellinger. 1990. Reproduction and development of two angel sharks, *Squatina squatina* and *S. oculata* (Pisces: Squatinidae), off Tunisian coasts: semi-delayed vitellogenesis, lack of egg capsules, and lecithotrophy. *Journal of Fish Biology*. 37(3):347–356.

Capapé, C., Diatta, Y., Diop, M.P., Vergne, Y. and O. Guelorget. 2006. Reproductive biology of the smooth hound, *Mustelus mustelu*s (Chondrichthyes: Triakidae) from the coast of Senegal (eastern tropical Atlantic). *Cybium*. 30(3):273–282.

Carey, F. G., and J.V. Scharold. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology*, 106:329–342.

Cariani, A., Messinetti, S., Ferrari, A., Arculeo, M., Bonello, J.J., Bonnici, L., Cannas, R., Carbonara, P., Cau, A., Charilaou, C. and El Ouamari, N., 2017. Improving the conservation of Mediterranean chondrichthyans: the ELASMOMED DNA barcode reference library. *PloS one*, 12(1), p.e0170244.

Carlson, J.K., Goldman, K.J. and C.G. Lowe. 2004. Metabolism, energetic demand, and endothermy. *Biology of sharks and their relatives. CRC Press, Boca Raton*. 203–224.

Cartamil, D. P., Vaudo, J. J., Lowe, C. G., Wetherbee, B. M., and K.H. Holland. 2003. Diel movement patterms of the Hawaiian stingray, *Dasyatis lata*: implications for the ecological interactions between sympatric elasmobranch species. *Marine Biology*, 142(5): 841–847.

Cerrato, R.M. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences*. 47(7):1416–1426.

Chapman, D.D., Prodöhl, P.A., Gelsleichter, J., Manire, C.A. and M.S. Shivji. 2004. Predominance of genetic monogamy by females in a hammerhead shark, *Sphyrna tiburo*: implications for shark conservation. *Molecular Ecology*. 13(7):1965–1974.

Chapman, D.D., Pikitch, E.K., Babcock, E. and M.S. Schivji. 2005. Marine reserve design and evaluation using automated acoustic telemetry: A case-study involving coral reef-associated sharks in the Mesoamerican Caribbean. *Marine Technology Society Journal*. 39(1):42–55.

Chapman, D.D., Shivji, M.S., Louis, E., Sommer, J., Fletcher, H. and P.A. Prodöhl. 2007.

Virgin birth in a hammerhead shark. *Biology Letters*. 3(4):425–427.

Chapman, D.D., Firchau, B. and M.S. Shivji. 2008. Parthenogenesis in a large-bodied requiem shark, the blacktip *Carcharhinus limbatus*. *Journal of Fish Biology*. 73(6):1473–1477.

Chapman, B.B., Hulthén, K., Brodersen, J., Nilsson, P. A, Skov, C., Hansson, L.A. and C. Brönmark. 2012. Partial migration in fishes: causes and consequences. *Journal of Fish Biology*. 81(2):456–78.

Chesson, J. 1978. Measuring preference in selective predation. *Ecology*. 59(2): 211-215.

Chidlow, J.A., Simpfendorfer, C.A. and G.R. Russ. 2007. Variable growth band deposition leads to age and growth uncertainty in the western wobbegong shark, *Orectolobus hutchinsi*. *Marine and Freshwater Research*. 58(9):856–865.

Chin, A., Simpfendorfer, C., Tobin, A. and M. Heupel. 2013. Validated age, growth and reproductive biology of *Carcharhinus melanopterus,* a widely distributed and exploited reef shark. *Marine and Freshwater Research*. 64(10):965–975.

Claramunt, R. M., Jonas, J. L., Fitzsimons, J. D., and J.E. Marsden. 2005. Influences of spawning habitat characteristics and interstitial predators on lake trout egg deposition and mortality. *Transactions of the American Fisheries Society*, 134(4): 1048–1057.

Clarke, S. 2002. *Trade in Asian dried seafood: characterization, estimation and implications for conservation*. Bronx, NY, USA: Wildlife Conservation Society.

Clark BM, Massie V, Hutchings K, Brown E, Biccard A, Laird M, Harmer R, Makhosonke A, Wright A and J. Turpie. 2017. The State of Saldanha Bay and Langebaan Lagoon. 2017, Technical Report. Report No. AEC 1741/1 prepared by Anchor Environmental Consultants (Pty) Ltd for the Saldanha Bay Water Quality Forum Trust, Cape Town

Compagno, L.J. V. 1984. F.A.O species catalogue.4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Carcharhiniformes. *F.A.O. Fish. Synop.* 125(2):250–655.

Conrath, C.L. and J.A. Musick. 2002. Reproductive biology of the smooth dogfish, *Mustelus canis,* in the northwest Atlantic Ocean. *Environmental Biology of Fishes*. 64(4):367–377.

Conrath, C.L., Gelsleichter, J. and J.A. Musick. 2002. Age and growth of the smooth dogfish (*Mustelus canis*) in the northwest Atlantic Ocean. *Fishery Bulletin*. 100(4):674–682.
Conrath, C.L. 2005. Reproductive biology. *FAO Fisheries Technical Paper (FAO)*.

Constantini, M., Bernardini, M., Cordone, P., Guilianni, P.G. and G. Orel. 2000. Observations on fishery, feeding habits and reproductive biology of *Mustelus mustelus* (Chondrichthyes, Triakidae) in Northern Adriatic Sea. *Biologica Marina Mediterranean*. 7(1):427–432.

Cortés, E. 1998. Demographic analysis as an aid in shark stock assessment and management. *Fisheries Research*. 39:199–208.

Cortés, E. 1999. A stochastic stage-based population model of the sandbar shark in the western north Atlantic. In *Life in the slow lane: ecology and conservation of long lived marine animals*. J.A. Musick, Ed. American Fisheries Society Symposium 23, Bethesda, MD: 115–136

Cortés, E. 2000. Life history patterns and correlations in sharks. *Reviews in Fisheries Science*. 8(4):299–344.

Cortés, E. 2002. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation biology*. 16(4):1048–1062.

Cortés, E. 2008. Comparative life history and demography of pelagic sharks. In *Sharks of the open ocean: biology, fisheries and conservation*. M.D. Camhi, E.K. Pikitch, and E.A. Babcock, Eds. Oxford, United Kingdom: Blackwell Publishing. 309–322.

Cortés, F., Jaureguizar, A. J., Menni, R. C., and R.A. Guerrero. 2011. Ontogenetic habitat preferences of the narrownose smooth-hound shark, *Mustelus schmitti*, in two Southwestern Atlantic coastal areas. *Hydrobiologia*, 661(1): 445–456.

da Silva, C. 2007. The status and prognosis of the smoothhound shark (*Mustelus mustelus*) fishery in the southeastern and southwestern Cape coasts, South Africa. Rhodes University.

da Silva, C. and M. Bürgener. 2007. South Africa's demersal shark meat harvest. *Traffic Bulletin*. 21(2):55–56.

da Silva, C. and M.E. McCord. 2013. Blackspotted smoothhound *Mustelus mustelus*. In *South African Marine Linefish Species profiles*. Special Publication No. 9. B.Q. Mann, Ed. Durban, South Africa: Oceanic Research Institute. 289–290.

da Silva, C., Booth, A., Dudley, S., Kerwath, S., Lamberth, S., Leslie, R., McCord, M., Sauer, W.H.H. and T. Zweig. 2015. The current status and management of South Africa's chondrichthyan fisheries. *African Journal of Marine Science*. 37(2):233–248.

DAFF. 2010. *Status of South African Marine Fishery Resources.* Department of Agriculture, Forestry and Fisheries.

Daly-Engel, T.S., Grubbs, R.D., Holland, K.N., Toonen, R.J. and B.W. Bowen. 2006. Assessment of multiple paternity in single litters from three species of carcharhinid sharks in Hawaii. *Environmental Biology of Fishes*. 76(2–4):419–424.

Daly-Engel, T.S., Grubbs, R.D., Bowen, B.W. and R.J. Toonen. 2007. Frequency of multiple paternity in an unexploited tropical population of sandbar sharks (*Carcharhinus plumbeus*). *Canadian Journal of Fisheries and Aquatic Sciences*. 64(2):198–204.

Daly-Engel, T.S., Grubbs, R.D., Feldheim, K.A., Bowen, B.W. and R.J. Toonen. 2010. Is multiple mating beneficial or unavoidable? Low multiple paternity and genetic diversity in the shortspine spurdog *Squalus mitsukurii*. *Marine Ecology Progress Series*. 403:255–267.

Davenport, S. and J.D. Stevens. 1988. Age and growth of two commercially imported sharks (*Carcharhinus tilstoni* and *C. sorrah*) from Northern Australia. *Marine and Freshwater*

Research. 39(4):417–433.

Davidson, L.N.K., Krawchuk, M.A. and N.K. Dulvy. 2015. Why have global shark and ray landings declined: improved management or overfishing? *Fish and Fisheries*. 1–21.

Davies, D.H. 1964. *About sharks and shark attack*. S. and Shooter, Ed. Pietermaritzburg.

Day, J.H. 1959. The biology of Langebaan Lagoon: a study of the effect of shelter from wave action. *Transactions of the Royal Society of South Africa*. 35(5):475–547.

Delany, M.J. 1978. Introduction: marking animals for research. In *Animal Marking*. Macmillan Education UK. 1–10.

Denny, C.M.M. and R.C. Babcock. 2004. Do partial marine reserves protect reef fish assemblages? *Biological Conservation*. 116(1):119–129.

Denny, C.M., Willis, T.J. and R.C. Babcock. 2004. Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status. *Marine Ecology Progress Series*. 272:183–190.

Dewar, H., Mous, P. J., Domeier, M., Muljadi, A., Pet, J., and J. Whitty. 2008. Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. *Marine Biology*, 155(2): 121–133.

DeWitt, C. B., and R.M. Friedman. 1979. Significance of skewness in ectotherm thermoregulation. *American Zoologist*, 19 (1): 195–209.

Dicken, M.L., Smale, M.J. and A.J. Booth. 2006. Spatial and seasonal distribution patterns of ragged-tooth shark *Carcharias taurus* along the coast of South Africa. *South African Journal of Marine Science*. 28(3–4):603–616.

Dicken, M., Smale, M.J. and A.J. Booth. 2007. Spatial and seasonal distribution patterns of juvenile and adult raggedtooth sharks (*Carcharias taurus*) tagged off the East Coast of South Africa. *Marine and Freshwater Research*. 58:127–134.

Digirolamo, A.L., Gruber, S.H., Pomory, C. and W.A. Bennett. 2012. Diel temperature patterns of juvenile lemon sharks *Negaprion brevirostris*, in a shallow-water nursery. *Journal of fish biology*. 80(5):1436–1448.

Dingle, R.D.H. 1996. *Migration: the biology of life on the move.* New York: Oxford University Press:1- 475
Dingle, H., and V.A. Drake. 2007. What Is Migration ?. *Bioscience. 57*(2): 113–121.

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.L., Francis, M.P., C.M. Pollock. 2014. Extinction risk and conservation of the world's sharks and rays. *Elife*. 3.

Dulvy, N. K., Simpfendorfer, C. A., Davidson, L. N., Fordham, S. V., Bräutigam, A., Sant,

G., and D.J. Welch. 2017. Challenges and priorities in shark and ray conservation. *Current Biology*, *27*(11), R565-R572.

Ebert, D. A. 1991. Observations on the predatory behaviour of the sevengill shark *Notorynchus cepedianus*. *South African Journal of Marine Science*, 11(1): 455–465.

Ebert, D.A. and T.B. Ebert. 2005. Reproduction, diet and habitat use of leopard sharks, T*riakis semifasciata* (Girard), in Humboldt Bay, California, USA. *Marine and Freshwater Research*. 56(8):1089–1098.

Ebert, D.A., Compagno, L.J. V and P.D. Cowley. 2006. Reproductive biology of catsharks (Chondrichthyes: Scyliorhinidae) off the west coast of southern Africa. *ICES Journal of Marine Science*. 63:1053–1065.

Ebert, D.A. and K.E. van Hees. 2015. Beyond Jaws: rediscovering the "lost sharks" of southern Africa. *African Journal of Marine Science*. 37(2):141–156.

Economakis, A.E. and P.S. Lobel. 1998. Aggregation behavior of the grey reef shark , *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. (4):129–139.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T., Berkhout, J. and C.D. Buxton. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature.* 506 (7487):216–220.

Espinoza, M., Farrugia, T.J. and C.G. Lowe. 2011. Habitat use, movements and site fidelity of the gray smooth-hound shark (*Mustelus californicus* Gill 1863) in a newly restored southern California estuary. *Journal of Experimental Biology*. 401(1-2):63–74.

Everett, B.I., Cliff, G., Dudley, S.F.J., Wintner, S.P. and R.P. van der Elst. 2015. Do sawfish Pristis spp. represent South Africa's first local extirpation of marine elasmobranchs in the modern era? *African Journal of Marine Science*. 37(2):275–284.

FAO. 2011. Review of the state of world marine fishery resources. *FAO Fisheries and Aquaculture Technical Paper, Rome*. 569:334.

Fernández, S.S. 2011. Empirical evaluation of the effectiveness of South Africa's Marine Protected Area network in representing fish communities. University of Cape Town.

Feldheim, K.A., Gruber, S.H. and M.V. Ashley. 2002. The breeding biology of lemon sharks at a tropical nursery lagoon. *Proc. R. Soc. Lond. B*. 269(1501):1655–1661.

Feldheim, K.A., Chapman, D.D., Sweet, D., Fitzpatrick, S., Prodöl, P.A., Shivji, M.S. and B. Snowden. 2010. Shark virgin virth produces multiple, viable offspring. *Journal of Heredity*. 101(3):374–377.

Ferretti, F., Myers, R.A., Serena, F. and H.K. Lotze. 2008. Loss of Large Predatory Sharks from the Mediterranean Sea. *Conservation Biology*. 22:952–964.

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. and H.K. Lotze. 2010. Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*. 13(8):1055–1071.

Field, I.C., Meekan, M.G., Buckworth, R.C. and C.J.A. Bradshaw. 2009. Susceptibility of sharks, rays and chimaeras to global extinction. *Advances in Marine Biology*. 56:275–363.

Field, I.C., Meekan, M.G., Speed, C.W., White, W. and C.J.A. Bradshaw. 2011. Quantifying movement patterns for shark conservation at remote coral atolls in the Indian Ocean. *Coral Reefs*. 30(1):61–71.

Finstad, B., Okland, F., Bjorn, P. A., and R.S. McKinley. 2005. Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology*, *66*, 86–96.

Foerster, R. E. 1942. Dogfish tagging – preliminary results. Progress Report Fisheries Research Board of Canada, *Nanaimo* 53: 12-1 3.

Francis, M.P. and J.T. Mace. 1980. Reproductive biology of *Mustelus lenticulatus* from Kaikoura and Nelson. *New Zealand Journal of Marine and Freshwater Research*. 14(3):303–311.

Francis, R. 1988. Maximum likelihood estimation of growth and growth variability from tagging data. *New Zealand Journal of Marine and Freshwater Research*. 22(1):43–51.

Francis, M.P. 1989. Exploitation rates of rig (*Mustelus lenticulatus*) around the South Island of New Zealand. *New Zealand Journal of Marine and Freshwater Research*. 23(2):239–245.

Francis, M.P. and C. Ó. Maolagáin. 2000. Age, growth and maturity of a New Zealand endemic shark (*Mustelus lenticulatus*) estimated from vertebral bands. *Marine and Freshwater Research*. 51(1):35–42.

Fraser, D.F. and R.D. Cerri. 1982. Experimental evaluation of predator-prey relationships in a patch environment: consequences for habitat use patters in minnows. *Ecology*. 63(2):307–313.

Freer, D.W.L. and C.L. Griffiths. 1993. The fishery for, and general biology of, the St. Joseph *Callorhinchus capensis* [Dumeril] off the south-western Cape, South Africa. 13(1):63–74.

Fréon, P. and O.A. Misund. 1999. *Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment.* Oxford: Blackwell Science.

Fréon, P., Coetzee, J.C., van der Lingen, C.D., Connell, A.D., O'Donoghue, S.H., Roberts, M.J., Demarcq, H., Attwood, C.G., Lamberth, S.J. and L. Hutchings. 2010. A review and tests of hypotheses about causes of the KwaZulu-Natal sardine run. *African Journal of Marine Science*. 32(2):449–479.

Froese, R., Zeller, D., Kleisner, K. and D. Pauly. 2012. What catch data can tell us about the status of global fisheries. *Marine biology*. 159(6):1283–1292.

Gallucci, V.F., Taylor, I.G. and Erzini, K. 2006. Conservation and management of exploited

shark populations based on reproductive value. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 931–942.

Garla, R.C., Chapman, D.D., Shivji, M.S., Wetherbee, B.M. and Amorim, A. F. 2006a. Habitat of juvenile Caribbean reef sharks, *Carcharhinus perezi*, at two oceanic insular marine protected areas in the southwestern Atlantic Ocean: Fernando de Noronha Archipelago and Atol das Rocas, Brazil. *Fisheries Research*. 81(2–3):236–241.

Garla, R.C., Chapman, D.D., Wetherbee, B.M. and Shivji, M. 2006b. Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. *Marine Biology*. 149(2):189–199.

Gaylord, B., Gaines, S.D., Siegel, D.A. and M.R. Carr. 2005. Marine reserves exploit population structure and life history in potentially improving fisheries yields. *Ecological Applications*. 15(6):2180–2191.

Gell, F.R. and C.M. Roberts. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology and Evolution*. 18:448–455.

Gerking, S.D. 1953. Evidence for the concepts of home range and territory in stream fishes. *Ecology*. 34: 347–365.

Godin, J.G.J. 1997. Behavioural ecology of fishes: adaptations for survival and reproduction. *Behavioural Ecology of Teleost Fishes*. 1-9

Goethel, D.R., Quinn, T.J. and S.X. Cadrin. 2011. Incorporating spatial structure in stock assessment: movement modeling in marine fish population dynamics. *Reviews in Fisheries Science*. 19(2):119–136.

Goosen, A.J.J. and M.J. Smale. 1997. A preliminary study of age and growth of the smoothhound shark *Mustelus mustelus* (Triakidae). *South African Journal of Marine Science*. 18(1):85–91.

Götz, A., Kerwath, S.E. and C.G. Attwood. 2013. A step-by-step framework to assess benefits of established temperate marine protected areas. *South African Journal of Science*. 109(1–2):1–9.

Greenstone, J. 2013. Moving towards self-governance: Why the future of management may lie with fisher cooperatives. *Fishing Industry Handbook*. 41st Edition. 332–333.

Griffiths, A.M., Jacoby, D.M.P., Casane, D., McHugh, M., Croft, D.P., Genner, M.J. and D.W. Sims. 2011. First analysis of multiple paternity in an oviparous shark, the small-spotted catshark (*Scyliorhinus canicula* L.). *Journal of Heredity*. 103(2):166–173.

Griffiths, M.H. 2000. Long-term trends in catch and effort for the Cape commercial linefishery: snapshots of the 20th Century. *South African Journal of Marine Science*. 22(1):81–110.

Griffiths, M.H., Wilke, C., Penney, A.J. and Y. Melo. 2002. Life history of the white

stumpnose *Rhabdosargus globiceps* (Pisces: Sparidae) off South Africa. *South African Journal of Marine Science*. 24(1):281–300.

Groeneveld, J.C.A., Cliff, G.B., Dudley, S.F.J.C. and A.J.A. Foulis. 2014. Population structure and biology of shortfin mako, *Isurus oxyrinchus*, in the south-west Indian Ocean. *Marine and Freshwater Research*.

Groot, T.V.M., Bruins, E. and J.A.J. Breeuwer. 2003. Molecular genetic evidence for parthenogenesis in the Burmese python, *Python molurus bivittatus*. *Heredity*. 90(2):130–135.
Grubbs, R. D. 2010. Ontogenetic shifts in movements and habitat use. In *Sharks and their relatives II: Biodiversity, adaptive physiology, and conservation. CRC Press, Boca Raton*. 319–350.

Grubbs, R.D., Musick, J.A., Conrath, C.L. and J.G. Romine. 2007. Long-term movements, migration, and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. In *American Fisheries Society Symposium* (Vol. 50, p. 87). American Fisheries Society.

Gruber, S. H., Nelson, D. R., and J.F. Morrissey. 1988. Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. *Bulletin of Marine Science*, 43(1): 61–76.

Gubili, C., Duffy, C.A., Cliff, G., Wintner, S.P., Shivji, M., Chapman, D., Bruce, B.D., Martin, A.P., Sims, D.W., Jones, C.S. and L.R. Noble. 2012. Application of molecular genetics for conservation of the white shark, *Carcharodon carcharias*, L. 1758. In *Global Perspectives on the Biology and Life History of the White Shark*. Florida: CRC Press, Boca Raton. 357–380.

Guttridge, T.L., Gruber, S.H., Franks, B.R., Kessel, S.T., Gledhill, K.S., Uphill, J., Krause, J. and D.W. Sims. 2012. Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Marine Ecology Progress Series*. 445:279–291.

Hammerschlag, N., Gallagher, A. J. and Lazarre, D.M. 2011. A review of shark satellite tagging studies. *Journal of Experimental Marine Biology and Ecology*. 398(1–2):1–8.
Harden Jones, F.R. 1968. *Fish migration*. London, UK: Edward Arnold.

Hareide, N.R., Carlson, J., Clarke, M., Clarke, S., Ellis, J., Fordham, S., Fowler, S., Pinho, M., Raymakers, C., Serena, F. and B. Seret. 2007. European shark fisheries: a preliminary investigation into fisheries conversion factors, trade products, markets and management measures. *European Elasmobranch Association*.1-57

Harris, J. E. 1952. A note on the breeding season, sex ratio and embryonic development of the dogfish *Scyliorhinus canicula* (L.). *Journal of the Marine Biological Association of the United Kingdom*, 31(2): 269–275.

Harry, A.V. 2018. Evidence for sytemic age underestimation in shark and ray ageing studies.

Fish and Fisheries. 19 (2): 185-200.

Hawkins, A.D., MacLennan, D.N., Urquhart, G.G. and Robb, C. 1974. Tracking cod, *Gadus morphua* L., in a Scottish sea loch. *Journal of Fish Biology*. 6 (3):225–236.

Hearn, A., Ketchum, J., Klimley, A., Espinoza, E. and C. Peñaherrera. 2010. Hotspots within hotspots? Hammerhead shark movements around Wolf Island, Galapagos Marine Reserve. *Marine Biology*. 157(9):1899–1915.

Hedger, R.D., Næsje, T.F., Cowley, P.D., Thorstad, E.B., Attwood, C.G., Økland, F., Wilke, C.G. and S.E. Kerwath. 2010. Residency and migratory behaviour by adult *Pomatomus saltatrix* in a South African coastal embayment. *Estuarine, Coastal and Shelf Science*. 89(1):12–20.

Heithaus, M.R., Dill, L.M., Marshall, G.J. and B. Buhleier. 2002. Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Marine Biology*. 140 (2):237–248.

Heithaus, M.R., Hamilton, I.M., Wirsing, A.J. and L.M. Dill. 2006. Validation of a randomization procedure to assess animal habitat preferences: microhabitat use of tiger sharks in a seagrass ecosystem. *Journal of Animal Ecology*. 75(3):666–676.

Hendry, A.P. 2004. To sea or not to sea: anadromy versus non-anadromy in salmonids. In *Evolution illuminated: salmon and salmonids*. A.P. Hendry and S.C. Stearns, Eds. New York, USA: Oxford University Press. 92–125.

Heupel, M.R. and R.E. Hueter. 2002. Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. *Marine and Freshwater Research*. 53(2):543–550.

Heupel, M.R., Simpfendorfer, C.A. and R.E. Hueter. 2004. Estimation of Shark Home Ranges using Passive Monitoring Techniques. *Environmental Biology of Fishes*. 71:135–142.

Heupel, M.R. and C.A. Simpfendorfer. 2005a. Using acoustic monitoring to evaluate MPAs for shark nursery areas: the importance of long-term data. *Marine Technology Society Journal*. 39(1):10–18.

Heupel, M. R. and C.A. Simpfendorfer. 2005b. Quantitative analysis of aggregation behavior in juvenile blacktip sharks. *Marine Biology*, 147, 1239–1249.

Heupel, M.R. and C.A. Simpfendorfer. 2008. Movement and distribution of young bull sharks Carcharhinus leucas in a variable estuarine environment. *Aquatic Biology*. 1(3): 277-289.

Heupel, M. R., Jayson M. Semmens, and A. J. Hobday. 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research.* 57 (1): 1-13.

Heupel, M.R., Carlson, J.K. and C.A. Simpfendorfer. 2007. Shark nursery areas: concepts,

definition, characterization and assumption. *Marine Ecology Progress Series*. 337:287–297.

Heupel, M.R., Williams, A.J., Welch, D.J., Ballagh, A., Mapstone, B.D., Carlos, G., Davies, C. and C.A. Simpfendorfer. 2009. Effects of fishing on tropical reef associated shark populations on the Great Barrier Reef. *Fisheries Research*. 95(2–3):350–361.

Hight, B. V and C.G. Lowe. 2007. Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: Evidence for behavioral thermoregulation? *Journal of Experimental Marine Biology and Ecology*. 352(1):114–128.

Hockersmith, E.E. and J.W. Beeman. 2012. A history of telemetry in fishery research. *Telemetry techniques: a user guide for fisheries research. Bethesda, Maryland: American Fisheries Society*. 542.

Holden, M.J., 1973. Are long-term sustainable fisheries for elasmobranchs possible?. Rapports et procès-verbaux des réunions, International Council for the Exploration of the Sea. 164: 360-367.

Holeton, G. and N. Heisler. 1978. Acid-base regulation by bicarbonate exchange in the gills after exhausting activity in the larger spotted dogfish *Scyliorhinus stellaris*. *Fishery Bulletin*. 21(56):84–96.

Holland, K.N., Lowe, C.G., Peterson, J.D. and A. Gill. 1992. Tracking coastal sharks with small boats: hammerhead shark pups as a case study. *Australian Journal of Marine and Freshwater Research*. 43:61–66.

Holland, K. N., Wetherbee, B. M., Peterson, J. D., and C.G. Lowe. 1993. Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia*, 2: 495–502.

Holland, K. N., Wetherbee, B. M., Lowe, C. G., and C.G. Meyer. 1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. *Marine Biology*, 134: 665–673.

Hopkins, T.E. and J.J.J. Cech. 2003. The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. *Environmental Biology of Fishes*. 66:279–291.

Hurley, P.C.F. 1998. A review of the fishery for pelagic sharks in Atlantic Canada. *Fisheries Research*. 39 (2):107–113.

Hussey, N.E., McCarthy, I.D., Dudley, S.F.J. and B.Q. Mann. 2009. Nursery grounds, movement patterns and growth rates of dusky sharks, *Carcharhinus obscurus*: a long-term tag and release study in South African waters. *Marine and Freshwater Research*. 60:571–583.

Hussey, N.E., Wintner, S.P., Dudley, S.F.J., Cliff, G., Cocks, D.T. and A.M. MacNeil. 2010. Maternal investment and size-specific reproductive output in carcharhinid sharks. *Journal of Animal Ecology*. 79:184–193.

Huveneers, C., Stead, J., Bennett, M.B., Lee, K.A. and R.G. Harcourt. 2013. Age and growth determination of three sympatric wobbegong sharks: How reliable is growth band periodicity

in Orectolobidae? *Fisheries Research*. 147:413–425.

Jabado, R.W., Al Ghais, S.M., Hamza, W., Henderson, A.C., Spaet, J.L., Shivji, M.S. and R.H. Hanner. 2015. The trade in sharks and their products in the United Arab Emirates. *Biological Conservation*. 181:190–198.

Jacoby, D. M., Croft, D. P. and D.W. Sims. 2012. Social behaviour in sharks and rays: analysis, patterns and implications for conservation. *Fish and Fisheries*, 13(4): 399–417.

Jennings, S., Greenstreet, S., and J.Reynolds. 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*. 68(3):617–627.

Johnson, R., Bester, M.N., Dudley, S.F.J., Oosthuizen, W.H., Meyer, M., Hancke, L. and E. Gennari. 2009. Coastal swimming patterns of white sharks (*Carcharadon carcharias*) at Mossel Bay, South Afica. *Environmental Biology of Fishes*. 85:189–200.

Jonsson, B. and Jonsson, N., 1993. Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, 3(4), pp.348-365.

Jolly, K.A. and C.G. Attwood. 2011. Aspects of the biology and fishery of the blue shark (*Prionace glauca*) in the South African waters. MSc Thesis.University of Cape Town.
Kanyerere, G.Z., Weyl, O.L.F. and A.J. Booth. 2005. Growth, reproduction and population structure of *Diplotaxodon limnothrissa* in the southeast arm of Lake Malawi. *African Journal of Aquatic Science*. 30(1):37–44.

Kempster, R.M., Hart, N.S. and S.P. Collin. 2013. Survival of the stillest: predator avoidance in shark embryos. *PloS one*. 8(1):e52551. DOI: 10.1371/journal.pone.0052551.

Kennedy, J.S. 1985. Migration, behavioral and ecological. In *Migration: Mechanisms and Adaptive Significance. Contributions in Marine Science 27 (suppl).* V. 68. M.A. Rankin, Ed. Austin: Marine Science Institute, University of Texas. 5–26.

Kerwath, S.E., Götz, A., Attwood, C.G. and W.H.H. Sauer. 2008. The effect of marine protected areas on an exploited population of sex-changing temperate reef fish: an individual-based model. *African Journal of Marine Science*. 30(2):337–350.

Kerwath, S.E., Thorstad, E.B., Naesje, T.F., Cowley, P.D., Okland, F., Wilke, C. and Attwood, C.G. 2009. Crossing invisible boundaries: the effectiveness of the Langebaan lagoon marine protected area as a harvest refuge for a migratory fish species in South Africa. *Conservation Biology*. 23(3):653–661.

Kerwath, S.E., Winker, H., Götz, A. and C.G. Attwood. 2013. Marine protected area improves yield without disadvantaging fishers. *Nature communications*. 4:2347.

Ketchen, K.S. 1986. The spiny dogfish (*Squalus acanthias*) in the Northeast Pacific and a history of its utilization. *Canadian Special Publication of Fisheries and Aquatic Sciences*. 88:1–78.

Ketterson, E.D. and V.J. Nolan Jr. 1985.Intraspecific variation in avian migration: Evolutionary and regulatory aspects. In *Migration: mechanisms and adaptive significance.*

27: 553-579

Khallahi, B. 2004. Ecologie et biologie de l'émissole lisse *Mustelus mustelus* (Linné, 1758) sur les côtes de Mauritanie. PhD Thesis, Université de Bretagne Occidentale, Brest, France.

Killam, K.A. and G.R. Parsons. 1989. Age and growth of the blacktip shark, *Carcharhinus limbatus*, near Tampa Bay, Florida. *Fishery Bulletin*. 87(4):845–857.

Kimber, J.A., Sims, D.W., Bellamy, P.H. and A.B. Gill. 2009. Male–female interactions affect foraging behaviour within groups of small-spotted catshark, *Scyliorhinus canicula*. *Animal Behaviour*. 77(6):1435–1440.

Kinney, M.J. and C.A. Simpfendorfer. 2009. Reassessing the value of nursery areas to shark conservation and management. *Conservation letters*. 2:53–60.

Klimley, A. P. and D.R. Nelson. 1984. Diel movement patterns of the scalloped hammerhead shark(*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. *Behavioral Ecology*, 15(1): 45–54.

Klimley, A. P., Butler, S. B., Nelson, D. R., and A.T. Stull. 1988. Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* Griffith and Smith, to and from a seamount in the Gulf of California. *Journal of Fish Biology*, 33(5): 751–761.

Knip, D.M., Heupel, M.R. and C.A. Simpfendorfer. 2012. Evaluating marine protected areas for the conservation of tropical coastal sharks. *Biological Conservation*. 148(1):200–209.
Kock, A., O'Riain, M.J., Mauff, K., Meÿer, M., Kotze, D. and C. Griffiths.2013. Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. *PloS one*. 8(1):e55048.

Kohler, N.E. and P.A. Turner. 2001. Shark tagging : a review of conventional methods and studies. *Environmental Biology of Fishes*. 60:191–223.

Kroese, M. and W.H.H. Sauer 1998. Elasmobranch exploitation in Africa. *Marine and Freshwater Research*. 49:573–577.

Lack, D. 1944. The problem of partial migration. *Brit. Birds*. 37:122–130.

Lack, M. and G. Sant. 2009. Trends in global sharks catch and recent developments in management. *Traffic International*. 33. Available: http://www.traffic.org/fish/.

Lampert, K.P., Lamatsch, D.K., Fischer, P., Epplen, J.T., Nanda, I., Schmid, M. and M. Schartl. 2007. Automictic reproduction in interspecific hybrids of poeciliid fish. *Current Biology*. 17(22):1948–1953.

Laroche, K.R., Kock, A.A., Dill, L.M. and H.W. Oosthuizen. 2008. Running the gauntlet: a predator–prey game between sharks and two age classes of seals. *Animal Behaviour*. 76(6):1901–1917.

Larson, S., Christiansen, J., Griffing, D., Ashe, J., Lowry, D. and K. Andrews. 2011. Relatedness and polyandry of sixgill sharks, *Hexanchus griseus*, in an urban estuary. *Conservation Genetics*. 12(3):679–690.

Leathwick, J. R., Elith, J., and T. Hastie. 2006. Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. *Ecological Modelling*, 199(2): 188–196.

Litvinov, F.F. 2006. On the role of dense aggregations of males and juveniles in the functional structure of the range of the blue shark *Prionace glauca*. *Journal of Ichthyology*. 46(8):613–624.

Lombard, A.T., Strauss, T., Harris, J., Sink, K., Attwood, C.G. and L. Hutchings. 2005. South African National Spatial Biodiversity Assessment. *Technical Report 2004*. 4.

Lowe, C.G. and K.J. Goldman. 2001. Thermal and bioenergetics of elasmobranchs: bridging the gap. *Environmental Biology of Fishes*. 60:251–266.

MacCall, A.D. 1990. Dynamic geography of marine fish populations. *University of Washington Press*, Seattle, WA.

Maduna, S.N. 2017. Unravelling the mystery of the shark genus *Mustelus* in southern Africa using a multi-disciplinary approach. PhD Thesis, Stellenbosch University, South Africa.

Maduna, S.N., da Silva, C., Wintner, S.P., Roodt-Wilding, R. and Bester-van der Merwe, A.E. 2016. When two oceans meet: regional population genetics of an exploited coastal shark, *Mustelus mustelus*. *Marine Ecology Progress Series*. 544:183–196.

Maduna, S.N., Rossouw, C., da Silva, C., Soekoe, M., and A. E. Bester-van der Merwe. 2017. Species identification and comparative population genetics of four coastal houndsharks based on novel NGS-mined microsatellites. *Ecology and Evolution*. 7: 1462-1486

Maduna, S.N., van Wyk, J.H., da Silva, C., E. Gennari and A. E. Bester-van der Merwe. 2018. Evidence for sperm storage in common smoothhound shark (*Mustelus mustelus*) assessment in a single litter from South Africa. *Journal of Fish Biology*.DOI.1111/jfb.13565

Manire, C.A., Rasmussen, L.E.L., Hess, D.L. and R.E. Hueter. 1995. Serum steroid hormones and the reproductive cycle of the female bonnethead shark, *Sphyrna tiburo*. *General and comparative endocrinology*. 97(3):366–376.

Mann, B.Q. and E.M. Bullen. 2009. ORI/WWF-SA Tagging Project: Summary of tag and recapture data for smooth houndsharks (*Mustelus mustelus*) caught along the Southern African coast from 1984-2008. *ORI Data Report*. (2009/3):1–23.

Marino, I.A., Riginella, E., Cariani, A., Tinti, F., Farrell, E.D., Mazzoldi, C. and Zane, L., 2014. New molecular tools for the identification of 2 endangered smooth-hound sharks, Mustelus mustelus and Mustelus punctulatus. Journal of Heredity, 106(1), pp.123-130.

Matern, S.A., Cech, J.J. and T.E. Hopkins. 2000. Diel movements of bat rays, *Myliobatiscalifornica*, in Tomales Bay, California: evidence for behavioral thermoregulation? *Environmental Biology of Fishes*. 58:173–182.

Matich, P. and M.R. Heithaus. 2012. Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, *Carcharhinus leucas*. *Marine Ecology Progress Series*, 447, pp.165-178.

McAuley, R. B., Simpfendorfer, C. A., and N.G. Hall. 2007. A method for evaluating the impacts of fishing mortality and stochastic influences on the demography of two long-lived shark stocks. ICES Journal of Marine Science, 64(9): 1710-1722.

McCord, M.E. 2005. Aspects of the ecology and management of the soupfin shark (*Galeorhinus galeus)* in South Africa. Rhodes University.

McCord, M.E. and S.J. Lamberth. 2009. Catching and tracking the world's largest Zambezi (bull) shark *Carcharhinus leucas* in the Breede Estuary, South Africa: the first 43 hours. *African Journal of Marine Science*. 31(1):107–111.

McCullagh, P., and J.A. Nelder 1995. Generalized linear models. London: Chapman and Hall.

McFarlane, G.A., Wydoski, R.S. and E.D. Prince.1990. External tags and marks. In *Historical review of the development of external tags and marks. American Fisheries Society Symposium*. (7): 9–29.

McKibben, J. N., and D.R. Nelson. 1986. Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bulletin of Marine Science*, 38(1): 89–110.

Meekan, M., Bradshaw, C., Press, M., McLean, C., Richards, A., Quasnichka, S. and J. Taylor. 2006. Population size and structure of whale sharks (*Rhincodon typus*) at Ningaloo Reef Western Australia. *Marine Ecology Progress Series*. 319:275–285.
Milas, N.A. 1947. The synthesis of vitamin A and related products. *Vitamins and Hormones*. 5:1–38.

Montealegre-Quijano, S. and C.M. Vooren. 2010. Distribution and abundance of the life stages of the blue shark *Prionace glauca* in the Southwest Atlantic. *Fisheries Research*. 101(3):168–179.

Morrissey, J.F. and S.H. Gruber. 1993a. Habitat selection by juvenile lemon sharks, Negaprion brevirostris. *Environmental Biology of Fishes*. 38(4):311–319.
Morrissey, J.F. and Gruber, S.H. 1993b. Home range of juvenile lemon sharks, *Negaprion brevirostris*. *Copeia*. 2:425–434.

Moulton, P.L., Walker, T.I. and S.R. Saddlier. 1992. Age and growth studies of gummy shark, *Mustelus antarcticus* Gunther, and School Shark, *Galeorhinus galeus* (Linnaeus), from Souther Australian Waters. *Marine and Freshwater Research*. 43(5):1241–1267.

Mull, C.G., Lowe, C.G. and K.A. Young. 2010. Seasonal reproduction of female round stingrays (*Urobatis halleri*): steroid hormone profiles and assessing reproductive state. *General and Comparative Endocrinology*. 166(2):379–387.

Musick, J.A. and S. Musick. 2011. Sharks. *FAO Fisheries and Aquaculture Reviews and Studies, Rome Italy*. 13.

Nakano, H. 1994. Age, reproduction and migration of blue shark [*Prionace*] in the North Pacific. *Bulletin-National Research Institute of Far Seas Fisheries (Japan).* 31:141–256.

Natanson, L.J., Mello, J.J. and S.E. Campana. 2002. Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean. *Fisheries Bulletin*. 100:266–278.

Nédélec, C., and J. Prado. 1990. Definition and classification of fishing gear categories. Définition et classification des categories d'engins de péche. Definición y clasificación de las diversas categorías de artes de pesca. FAO Fisheries Technical Paper, (222).

Neill, W. H. 1979. Mechanisms of fish distribution in heterothermal environments. *American Zoologist*, 19(1): 305–317.

Nel, P. and G.M. Branch. 2013. Assessment of the abundance and distribution of burrowing sandprawns and mudprawns (*Callichirus* and *Upogebia* species) in Langebaan Lagoon, South Africa. *African Journal of Marine Science*. 35(2):195–208.

Nelson, D.R. 1978. *Telemetering techniques for the study of free-ranging sharks*.*Sensory biology of sharks, skates, and rays. Office of Naval Research, Department of the Navy, Government Printing Office, Arlington, Virginia.* 419-482.

Nelson, D.R., McKibben, J.N., Strong, W.R., Lowe, C.G., Sisneros, J.A., Shroeder, D.M. and R.J. Lavenberg, 1997. An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertigal migrator. *Environmental biology of fishes*, 49(4), 389-399

Nelson, D.R. and R.H. Johnson. 2014. Diel activity rhythms in the nocturnal, bottom-dwelling sharks , *Heterodontus francisci* and *Cephaloscyllium ventriosum*. 1970(4):732–739.

Newton, I. 2008. *The migration ecology of birds*. London: Academic Press.

Officer, R.A., Gason, A.S., Walker, T.I. and J.G. Clement. 1996. Sources of variation in counts of growth increments in vertebrae from gummy shark,(*Mustelus antarcticus*, and school shark, *Galeorhinus galeus*): implications for age determination. *Canadian Journal of Fisheries and Aquatic Sciences*. 53(8):1765–1777.

Oliver, S., Braccini, M., Newman, S.J. and E.S. Harvey. 2015. Global patterns in the bycatch of sharks and rays. *Marine Policy*. 54:86–97.

Olsen, A. M. 1954. The Biology, migration, and growth rate of the school shark, *Galeorhinus australis* (Macleay)(Carcharhanidae) in the South-eastern Australian Waters. *Marine and Freshwater Research*, 5(3): 353–410.

Olsen, M.W. 1975. *Avian parthenogenesis.* Beltsville (MD): USDA.
Padovani-Ferreira, B. and C.M. Vooren. 1991. Age, growth, and structure of vertebra in the school shark *Galeorhinus galeus* (Linnaeus, 1758) from southern Brazil. *Fishery Bull US*. 89:19–31.

Papastamatiou, Y.P., Lowe, C.A., Caselle, J.G. and A.M. Friedlander. 2009. Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. *Ecology*. 90(4):996–1008.

Papastamatiou, Y.P., Cartamil, D.P., Lowe, C.G., Meyer, C.G., Wetherbee, B.M. and K.N. Holland. 2011. Scales of orientation, directed walks and movement path structure in sharks. *Journal of Animal Ecology*. 80(4):864–874.

Papastamatiou, Y.P. and C.G. Lowe. 2012. An analytical and hypothesis-driven approach to elasmobranch movement studies. *Journal of Fish Biology*. 80(5):1342–1360.

Papastamatiou, Y.P., Meyer, C.G., Carvalho, C., Dale, J.J., Hutchinson, M.R. and K.N. Holland, K.N. 2013a. Partial migration in tiger sharks. *Bulletin of the Ecological Society of America*. 94(3):250–251.

Papastamatiou, Y.P., Meyer, C.G., Carvalho, F., Dale, J.J., Hutchinson, M.R. and K.N. Holland. 2013b. Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator. *Ecology*. 94(11):2595–2606.

Pardini, A.T., Jones, C.S., Noble, L.R., Kreiser, B., Malcolm, H., Bruce, B.D., Stevens, J.D., Cliff, G., Scholl, M.C., Francis, M. and C.A. Duffy. 2001. Sex-biased dispersal in great white sharks. *Nature*. 412(6843):139–140.

Parker, D., Winker, H., da Silva, C., and S.E. Kerwath 2017. Data reporting challenges associated with spanning across the IOTC/ ICCAT boundary: a case study of shortfin mako *Isurus oxyrinchus*. *Working Party Paper.* IOTC-2017-WPDCS13-14.

Parsons, G.R. 1993. Geographic variation in reproduction between two populations of the bonnethead shark, *Sphyrna tiburo*. *Environmental Biology of Fishes*. 38(1–3):25–35.

Passerotti, M.S., Andrews, A.H., Carlson, J.K., Wintner, S.P., Goldman, K.J. and L.J. Natanson. 2014. Maximum age and missing time in the vertebrae of sand tiger shark (*Carcharias taurus*): validated lifespan from bomb radiocarbon dating in the western North Atlantic and southwestern Indian Oceans. *Marine and Freshwater Research*. 65(8):674–687.

Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O. and J. Matthiopoulos. 2008. State-space models of individual animal movement. *Trends in Ecology and Evolution*. 23(2):87–97.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and Jr., T.F. 1998. Fishing down marine food webs. *Science*. 279(5352):860–863.
Pelc, R.A., Baskett, M.L., Tanci, T., Gaines, S.D. and Warner, R.R. 2009. Quantifying larval export from South African marine reserves. *Marine Ecology Progress Series*. 394:65–78.

Peres, M.B. and C.M. Vooren. 1991. Sexual development reproductive cycle, and fecundity of the school shark *Galeorhinus galeus* off southern Brazil. *Fishery Bulletin*. 89(4):655–667.

Peters, I.T., Sauer, W.H. and J.G. Field. 2000. *Mustelus mustelus*. In *South African Marine Linefish Status Reports*. B.Q. Mann, Ed. Durban, South Africa: Special Publication,Oceanographic Research Institute. 224–225.

Pough, F.H., Janis, C.M. and J.B. Heiser. 1999. *Vertebrate Life* (5th Edition). New Jersey: Prentice-Hall.

Pratt, J.H.L. 1993. The storage of spermatozoa in the oviducal glands of western North Atlantic sharks. In *The reproduction and development of sharks, skates, rays and ratfishes*. Netherlands: Springer. 139–149.

Pratt, H.L. and S. Tanaka. 1994. Sperm storage in male elasmobranchs: a description and survey. *Journal of Morphology*. 219(3):297–308.

Pratt Jr, H.L. and J.C. Carrier. 2001. A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. *Environmental Biology of Fishes*. 60(1–3):157–188.

Prager, M. H., and J.M. Hoenig. 1989. Superposed epoch analysis: a randomization test of environmental effects on recruitment with application to chub mackerel. *Transactions of the American Fisheries Society*. *118*(6): 608-618.

Prince, J.D. 2005. Gauntlet Fisheries for Elasmobranchs- the secret of sustainable shark fisheries. *Journal of Northwest Atlantic Fisheries Science*. 35:407–416.

Punt, A.E., Pribac, F., Taylor, B.L. and T.I. Walker. 2005. Harvest strategy evaluation for school and gummy shark. *Journal of Northwest Atlantic Fisheries Science*. 35:387–406.

Puttick, G.M. 1977. Spatial and temporal variations in inter-tidal animal distribution at Langebaan Lagoon, South Africa. *Transactions of the Royal Society of South Africa*. 42(3–4):403–440.

Queiroz, N., Lima, F.P., Maia, A., Ribeiro, P.A., Correia, J.P. and A.M. Santos. 2005. Movement of blue shark, *Prionace glauca*, in the north-east Atlantic based on mark-recapture data. *Marine Biological Association of the United Kingdom. Journal*. 85(5):1107–1112.

Quinn, T.P. and R.D. Brodeur. 1991. Intra-specific variations in the movement patterns of marine animals. *American Zoologist*. 31(1):231–241.

Quinn, T.J. and R.B. Deriso. 1991. Quantitative fish dynamics. Oxford University Press, New York.

Rago, P.J., Sosebee, K.A., Brodziak, J.K.T., Murawski, S.A. and E.D. Anderson. 1998. Implications of recent increases in catches on the dynamics of Northwest Atlantic spiny dogfish (*Squalus acanthias*). *Fisheries Research*. 39(2):165–181.

Reid, J., Rathbun, G.B. and J.R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. *Marine Mammal Science*. 7(2):180–190.

Ricker, W.E. 1958. Maximum sustainable yields from fluctuating environments and mixed stocks. *Journal of the Fisheries Board of Canada.* 15(5):991-1006

Ripley, W.E. 1946. The soupfin shark and the fishery. *Calif. Div. Fish Game Fish. Bull.* 64:7–37.

Robbins, W.D., Hisano, M., Connolly, S.R. and J.H. Choat. 2006. Ongoing collapse of coral-reef shark populations. *Current Biology : CB*. 16(23):2314–2319.

Robinson, D.P., Baverstock, W., Al-Jaru, A., Hyland, K. and K.A. Khazanehdari. 2011. Annually recurring parthenogenesis in a zebra shark *Stegostoma fasciatum*. *Journal of Fish Biology*. 79(5):1376–1382.

Rountree, R. A., and K.W. Able. 1996. Seasonal abundance, growth, and foraging habits of juvenile smooth dogfish, *Mustelus canis*, in a New Jersey estuary. *Fishery Bulletin*, *94*(3): 522–534.

Saïdi, B., Bradaï, M.N. and A. Bouaïn. 2008. Reproductive biology of the smooth-hound shark *Mustelus mustelus* (L.) in the Gulf of Gabès (south-central Medeterranean Sea). *Journal of Fish Biology*. 72(6):1343–1354.

Saïdi, B., Bradaï, M.N. and A. Bouaïn. 2009. Reproductive biology and diet of *Mustelus punctulatus* (Risso, 1826)(Chondrichthyes: Triakidae) from the Gulf of Gabès, central Mediterranean Sea. *Scientia Marina*. 73(2):249–258.

Sanderson, G.C. 1966. The study of mammal movements : a review. *Journal of Wildlife Management*. 30(1):215–235.

Santos, R.R. and T. Grant. 2011. Diel pattern of migration in a poisonous toad from Brazil and the evolution of chemical defenses in diurnal amphibians. *Evolutionary Ecology*. 25(2):249–258.

Sauer, W.H.H., Roberts, M.J., Lipinski, M.R., Smale, M.J., Hanlon, R.T., Webber, D.M. and R.K. O'Dor. 1997. Choreography of the squid's "nuptial dance". *The Biological Bulletin*. 192(2):203–207.

Saville, K.J., Lindley, A.M., Maries, E.G., Carrier, J.C. and H.L. Pratt. 2002. Multiple paternity in the nurse shark, *Ginglymostoma cirratum*. *Environmental Biology of Fishes*. 63(3):347–351.

Schofield, G., Katselidis, K.A., Dimopoulos, P. and J.D. Pantis. 2008. Investigating the viability of photo-identification as an objective tool to study endangered sea turtle populations. *Journal of Experimental Marine Biology and Ecology*. 360(2):103–108.

Schofield, G., Bishop, C. M., Katselidis, K. A., Dimopoulos, P., Pantis, J. D., and G.C. Hays. 2009. Microhabitat selection by sea turtles in a dynamic thermal marine environment. *Journal of Animal Ecology*, *78*(1): 14–21.

Schuett, G.W., Fernandez, P.J., Chiszar, D. and H.M. Smith. 1998. Fatherless sons: a new type of parthenogenesis in snakes. *Fauna*. 1(3):20–25.

Shabangu, F.W., Coetzee, J.C., Hampton, I., Kerwath, S.E., de Wet, W.M. and A. Lezama-Ochoa. 2014. Hydro-acoustic Technology and its Application to Marine Science in South Africa. In *Reflections on the State of Reserch and Technology in South Africa's Marine and Maritime sectors, 122*. N. Funke, M. Claasen, R. Meissner, and K. Nortje, Eds. Pretoria, South Africa: The Council for Scientific and Industrial Research. 122–152. DOI: 978-0-7988-5617-1.

Shannon, L.V. and G.H. Stander. 1977. Physical and chemical characteristics of water in Saldanha Bay and Langebaan Lagoon. *Transactions of the Royal Society of South Africa*. 42(3–4):441–459.

Shotton, R. 1999. Case studies of the management of elasmobranch fisheries. *Food and Agriculture Organization of the United nations. Fisheries Technical Paper*. 1 and 2:920.

Simpfendorfer, C.A., Freitas, G.G., Wiley, T.R. and M.R. Heupel. 2005a. Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a Southwest Florida estuary. *Estuaries*. 28(1):78–85.

Simpfendorfer, C. A., Heupel, M.R., White, W.T. and N.K. Dulvy. 2011. The importance of research and public opinion to conservation management of sharks and rays: a synthesis. *Marine and Freshwater Research*. 62(6):518.

Simpfendorfer, C.A., and N.K. Dulvy. 2017. Bright spots of sustainable shark fishing. *Current Biology* 27 (3): R97-R98.

Simpfendorfer, C.A. 1999. Demographic analysis of the dusky shark fishery in southwestern Australia. Pages 149–160 in *Life in the slow lane: ecologyband conservation of long lived marine animals*. J.A. Musick, Ed. American Fisheries Society Symposium 23, Bethesda, MD.

Sims, D. W., Wearmouth, V. J., Southall, E. J., Hill, J. M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G.C., Righton, D., Metcalfe, J.D. and J.P. Nash. 2006. Hunt warm,rest cool:bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology*, 75(1): 176–190.

Sims, D. W., Witt, M. J., Richardson, A. J., Southall, E. J. and J.D. Metcalfe. 2006. Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proc. R. Soc. Lond. B*, 273(1591): 1195–1201.

Sims, D. W., Southall, E. J., Humphries, N. E., Hays, G. C., Bradshaw, C. J., Pitchford, J. W., James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A. and D. Morrit. 2008. Scaling laws of marine predator search behaviour. *Nature*, *451*(7182): 1098–1102.

Sims, D.W. 2003. Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks. *Journal of Fish Biology*. 63(Supplement A):53–73.

Sims, D.W. 2005. Differences in habitat selection and reproductive strategies of male and female sharks. *Sexual segregation in vertebrates: Ecology of the two sexes*. 127–147.

Sims, D.W. 2010. Tracking and analysis techniques for understanding free-ranging shark movements. In *Sharks and Their Relatives II*. J.C. Carrier, J.A. Musick, and M.R. Heithaus, Eds. Boca Raton, FL: CRC Press. 351–392.

Sims, D.W., Nash, J.P. and D. Morritt. 2001. Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. *Marine Biology*. 139(6):1165–1175.

Skomal, G.B. 2007. Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. 14:81–89.

Slooten, E., Dawson, S.M. and F. Lad. 1992. Survival rates of photographically identified Hector's dolphins from 1984 to 1988. *Marine Mammal Science*. 8(4):327–343.

Smale, M.J. and L.J.V. Compagno. 1997. Life history and diet of two southern african smoothhound sharks, *Mustelus mustelus* (Linnaeus, 1758) and *Mustelus palumbes* Smith, 1957 (Pisces: Triakidae). *South African Journal of Marine Science*. 18:229–248.

Smale, M.J., Sauer, W.H.H. and M.J. Roberts. 2001. Behavioural interactions of predators and spawning chokka squid off South Africa: towards quantification. *Marine Biology*. 139(6):1095–1105.

Smale, M.J., Dicken, M.L. and A.J. Booth. 2015. Seasonality, behaviour and philopatry of spotted ragged‐tooth sharks *Carcharias taurus* in Eastern Cape nursery areas, South Africa. *African Journal of Marine Science*. 37(2):219–231.

Smith, M.M. and P.C. Heemstra. 1986. Smith's Sea Fishes. Struik Publishers. Cape Town

Smith, S.E., Au, D.W. and C. Show. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research*. 49(7):663–678.

Solano-Fernandez, S., Attwood, C.G., Chalmers, R., Clark, B.M., Cowley, P.D., Fairweather, T., Fennessy, S.T., Goetz, A., Harrison, T.D., Kerwath, S.E. and S.J. Lamberth. 2012. Assessment of the effectiveness of South Africa's marine protected areas at representing ichthyofaunal communities. *Environmental Conservation*. 39(3):259–270.
Southern, H.N. 1938. The spring migration of the swallow over Europe. *British Birds*. 32:4–7.

Southwood, A. and L. Avens. 2010. Physiological, behavioral, and ecological aspects of migration in reptiles. *Journal of Comparative Physiology B*. 180(1):1–23.

Speed, C., Field, I., Meekan, M. and C. Bradshaw. 2010. Complexities of coastal shark movements and their implications for management. *Marine Ecology Progress Series*. 408:275–293.

Speed, C.W., Meekan, M.G., Field, I.C., McMahon, C.R., Abrantes, K. and C.J.A. Bradshaw. 2012. Trophic ecology of reef sharks determined using stable isotopes and telemetry. *Coral reefs*, 31(2):357-367.

Speed, C.W., Meekan, M.G., Field, I.C., McMahon, C.R., Harcourt, R.G., Stevens, J.D., Babcock, R.C., Pillans, R.D. and C.J.A. Bradshaw. 2016. Reef shark movements relative to a coastal marine protected area. Regional Studies in Marine Science. 3:58–66.

Stearns, S.C. 1967. Life-history tactics: a review of ideas. Quartery Review of Biology. 51:3–45.

Stearns, S.C. 1992. *The evolution of life histories*. V. 249. Oxford University Press Oxford.
Stefansson, G. and A.A. Rosenberg. 2006. Designing marine protected areas for migrating fish stocks. *Journal of Fish Biology*. 69 (S):66–78.

Stevens, J.D., 1999a. Shark tagging: a brief history of methods. Fish Movement and Migration, pp.65-68.

Stevens, J.D. 1999b. Variable resilience to fishing pressure in two sharks: the significance of different ecological and life history parameters. In *American Fisheries Society Symposium*. V. 23. 11–15.

Stevens, J.D., Bonfil, R., Dulvy, N.K. and P.A. Walker. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*. 57:476–494.

Sundström, L.F., Gruber, S.H., Clermont, S.M., Correia, J.P., de Marignac, J.R.C., Morrissey, J.F., Lowrance, C.R., Thomassen, L. and M.T. Oliveira. 2001. Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas,. *Environmental Biology of Fishes*. 60:225–250.

Tanaka, S. and Mizue, K. 1979. Studies on sharks, 15: Age and growth of Japanese dogfish Mustelus manazo Bleeker in the East China Sea. *Bulletin of the Japanese Society of Scientific Fisheries (Japan)*.

Teshima, K. 1974. Studies on sharks-7-Reproduction in female *Mustelus griseus*. 水産大学校研究報告. 22(3):197–206.

Thorstad, E.B., Økland, F., Rowsell, D. and R.S. McKinley. 2000. A new system for automatic recording of fish tagged with coded acoustic transmitters. *Fisheries Management and Ecology*. 7:281–294.

Thorstad, E.B., Rikardsen, A.H., Alp, A. and F. Økland. 2013. The use of electronic tags in fish research—an overview of fish telemetry methods. *Turkish Journal of Fisheries and Aquatic Sciences*. 13:881–896.

Tilney, R.L., Nelson, G., Radloff, S.E. and C.D. Buxton. 1996. Ichthyoplankton distribution and dispersal in the Tsitsikamma National Park marine reserve, South Africa. *South African Journal of Marine Science*. 17(1):1–14.

Towner, A.V., Wcisel, M.A., Reisinger, R.R., Edwards, D. and O.J. Jewell. 2013. Gauging the threat: the first population estimate for white sharks in South Africa using photo identification and automated Software. *PloS one*. 8(6):e66035.

Trefethen, P.S. 1956. Sonic equipment for tracking individual fish. *U.S.Fish and Wildlife Servie Special Science Report. Fisheries*. 179:1–11.
Trefethen, P.S., Dudley, J.W. and M.R. Smith. 1957. Ultrasonic tracer follows tagged fish. *Electronics*. 30(4):156–160.

Trefethen, P.S. and D.F. Sutherland. 1968. Passage of adult Chinook salmon through Brownlee Reservoir, 1960-1962. *U.S.Fish and Wildlife Service Fisheries Bulletin*. 67:35–45.

Tunley, K.L., Attwood, C.G., Moloney, C.L. and L. Fairhurst. 2009. Variation in population structure and life-history parameters of steentjies *Spondyliosoma emarginatum* : effects of exploitation and biogeography. *African Journal of Marine Science*. 31(2):133–143.

Vaudo, J., and C.G. Lowe. 2006. Movement patterns of the round stingray *Urubatis halleri* (Cooper) near a thermal outfall. *Journal of Fish Biology*, 68(6): 1756–1766.

Voegeli, F.A., Smale, M.J., Webber, D.M., Andrade, Y. and R.K. O'Dor. 2001. Ultrasonic telemetry, tracking and automated monitoring technology for sharks. In *The behavior and sensory biology of elasmobranch fishes: an anthology in memory of Donald Richard Nelson.* Netherlands, Springer.

von Bonde, C. 1934. Shark fishing as an industry. *Fisheries and Marine Biology Division, Union of South Africa Report 2*. 1–19.

Walker, T.I. 1998. Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research*. 49(7):553–572.

Wallman, H.L. and W.A. Bennett. 2006. Effects of parturition and feeding on thermal preference of Atlantic stingray, *Dasyatis sabina* [Lesueur]. *Environmental Biology of Fishes*. 75(3):259–267.

Watson, G. and M.J. Smale. 1998. Reproductive biology of shortnose spiny dogfish, *Squalus megalops*, from the Aghulas Bank, South Africa. *Marine and Freshwater Research*. 49(7):695–703.

Wearmouth, V.J. and D.W. Sims. 2008. Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Advances in marine biology*. 54:107–170.

Wearmouth, V.J., Southall, E.J., Morrit, D., Thompson, R.C., Cuthill, I.C., Partridge, J.C. and D.W. Sims. 2012. Year-round sexual harassment as a behavioral mediator of vertebrate population dynamics. 82(3):351–366.

West, G. and J.D. Stevens. 2001. Archival tagging of school shark, *Galeorhinus galeus*, in Australia: initial results. *Environmental Biology of Fishes*, 60: 283–298.

Wetherbee, B.M. 1996. Distribution and reproduction of the southern lantern shark from New Zealand. *Journal of fish biology*. 49(6):1186–1196.

Weyl, O.L.F. and A.J. Booth. 2008. Validation of annulus formation in otoliths of a temperate population of adult African sharptooth catfish *Clarias gariepinus* using fluorochrome marking of wild fish. *Journal of Fish Biology.* 73(4):1033-8.

White, W., Hall, N. and I. Potter. 2002. Size and age compositions and reproductive biology of the nervous shark *Carcharhinus cautus* in a large subtropical embayment, including an analysis of growth during pre-and postnatal life. *Marine Biology*. 141(6):1153–1164.

White, W.T., Platell, M.E. and I.C. Potter. 2001. Relationship between reproductive biology and age composition and growth in *Urolophus lobatus* (Batoidea: Urolophidae). *Marine Biology*. 138(1):135–147.

Wiirsig, B. and T.A. Jefferson.1990. Methods of photo-identification for small cetaceans. Report of the International Whaling Commision. Special Issue *12. 43-52*

Wilga, C.D., Motta, P.J. and C.P. Sanford. 2007. Evolution and ecology of feeding in elasmobranchs. In *Society for Integrative and Comparative Biology*. V. 47. Phoenix, Arizona, USA. 55–69. DOI: 10.1093/icb/icm029.

Wilson, C.D. and M.P. Seki. 1994. Biology and population characteristics of *Squalus mitsukurii* from a seamount in the central North Pacific Ocean. *Fishery Bulletin*. 92(4):851–864.

Wilson, S.G., Taylor, J.G. and A.F. Pearce. 2001. The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Nino/Southern Oscillation. *Environmental Biology of Fishes*, 61(1): 1-11.

Wintner, S.P. and G. Cliff. 1995. Age and growth determination of the blacktip shark, *Carcharhinus limbatus*, from the east coast of South Africa. *Fishery Bulletin*. 94:135–144.

Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S. and O.P. Jensen 2009. Rebuilding Global Fisheries. *Science*. 325 (5940):578–584.

Wourms, J.P. and L.S. Demski. 1993. The reproduction and development of sharks, skates, rays and ratfishes: introduction, history, overview, and future prospects. In *The reproduction and development of sharks, skates, rays and ratfishes*. Springer. 7–21.

Wynberg, R.P. and G.M. Branch. 1991. An assessment of bait-collecting for *Callianassa kraussi stebbing* in Langebaan Lagoon, Western Cape, and of associated avian predation. *South African Journal of Marine Science*. 11:141–152.

Yamaguchi, A., Taniuchi, T. and M. Shimizu. 1996. Age and Growth of the Starspotted Dogfish *Mustelus manazo* from Tokyo Bay, Japan. *Fisheries science*. 62(6):919–922.

Yamaguchi, A., Taniuchi, T. and M. Shimizu. 2000. Geographic variations in reproductive parameters of the starspotted dogfish, *Mustelus manazo*, from five localities in Japan and in Taiwan. *Environmental Biology of Fishes*. 57(2):221–233.

Yudin, K.G. and G.M. Cailliet. 1990. Age and growth of the gray smoothhound, *Mustelus californicus*, and the brown smoothhound, *M. henlei,* sharks from central California. *Copeia*. 1:191–204.